

Al No 8 / 44 Al. 16 / 1144

THE INDIAN ZOOLOGICAL MEMOIRS

ON INDIAN ANIMAL TYPES

(Initiated by the Late Professor K. N. Bahl)

EDITOR

Zoological Society of India

PROFESSOR R. V. SESHAIYA

(Head of the Department of Zoology,
Annamalai University, Annamalaiagar)

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SCOLIODON

(THE SHARK OF THE INDIAN SEAS)

BY

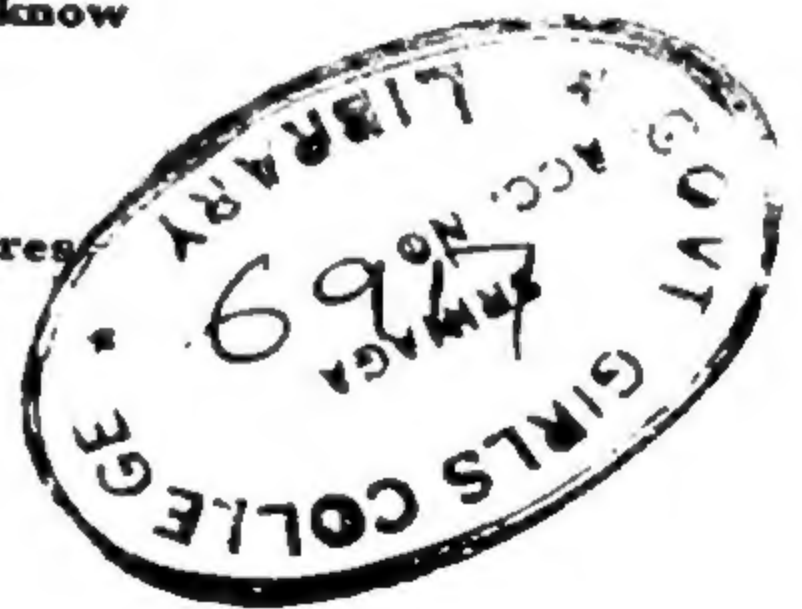
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REPRINTED

With 87 Coloured Plates and Text-figures



PUBLISHED BY:

THE ZOOLOGICAL SOCIETY OF INDIA
C/o ZOOLOGICAL SURVEY OF INDIA

34, CHITTARANJAN AVENUE
CALCUTTA-12

PRICE Rs. 4.50

JANUARY, 1958

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590

First Edition 1928
Second Edition 1948
Third Edition 1950
Fourth Edition 1952
Reprint 1958

Printed by Photo-offset by G. W. Lawrie & Co., Lucknow.

for

The Lucknow Publishing House, Lucknow.

FOREWORD

The series of monographs known as the "*Indian Zoological Memoirs on Indian Animal Types*" was started in 1926 by the late Professor K. N. Bahl who himself contributed the first volume dealing with *Pheretima*, the Indian earthworm. Subsequently, seven other volumes appeared under Prof. Bahl's editorship.

In 1954, the Zoological Society of India decided, in agreement with the late Prof. K. N. Bahl, to take on the responsibility of publishing these memoirs and a volume on the Sting Ray, *Dasyatis*, by Dr. M. Chandy, was entrusted to the Society's Editor, Dr. M. L. Bhatia of the Delhi University. Owing to unforeseen developments, however, that volume could not be brought out under the series.

Subsequently, in early 1957, the Society decided, with the consent of the author, to reprint the volume on the Indian river prawn, *Palaemon*, by Dr. D. S. S. Patwardhan, which was originally issued in 1937. This volume is now in the press.

Later on, Dr. (Miss) E. M. Thillayampalam also agreed to have the fifth reprint of her monograph on *Scoliodon*, the shark of the Indian seas, published under the auspices of the Society, and the volume is now presented herewith. The fourth edition, it may be added, was revised by the editor, the late Prof. Bahl.

Authors of several other memoirs in the series have also similarly agreed to revise their monographs for publication under the Society's auspices. On behalf of the Society, I heartily welcome this co-operation and am confident that by this means, a real service will be rendered to the cause of Indian zoology.

The Society will welcome co-operation from other prospective authors of new memoirs who are requested to contact the Society's Editor, Prof. R. V. Seshaiya of the Annamalai University, Annamalai-nagar.

Calcutta
30th November, 1957.

M. L. ROONWAL,
President,
Zoological Society of India.

PREFACE

The study of Zoology in Indian Universities was for several years handicapped for want of manuals dealing with Indian animal types, and students of animal morphology had to depend almost entirely on the description of foreign animal types contained in British text-books. To meet this long-felt need, the late Prof. K. N. Bahl, in his Presidential Address to the Zoology Section of XI session of the Indian Science Congress Association held in Bangalore in 1924, suggested the publication of a series of memoirs on Indian animal types. Two years later, Prof. Bahl initiated the publication of the now well-known Series of the Indian Zoological Memoirs with his monograph on the common Indian earthworm, *Pheretima*, as Memoir No. 1. Seven other Memoirs appeared in the series under the editorship of the late Prof. Bahl, all of which had very appreciative reception in Zoological circles.

The publication of the Indian Zoological Memoirs is now continued by the Zoological Society of India. A reprint of the Memoir on *Palaemon* by Dr. S. S. Patwardhan, which has been out of print for some time, is in the press. This is now followed by a reprint of the Memoir on *Scoliodon* by Dr. Thillayampalam, as publication No. II in the new series. It is also hoped to issue a revised edition of the Memoir on the Indian sea-urchin, *Salmacis*, by Prof. R. Gopala Aiyar. Further publications including new Memoirs are expected to appear in due course.

My thanks are due to Dr. M. L. Roonwal, President, Zoological Society of India, Dr. B. S. Chauhan, Convener, and Prof. P. N. Ganapati, Member of the Indian Zoological Memoirs Committee of the Zoological Society of India for their untiring efforts for realising the objectives of the Committee.

Annamalai University,
Annamalainagar,
November 29, 1957.

R. V. SESHAIYA,
Editor,
Zoological Society of India.



AUTHOR'S PREFACE

When the study of Zoology was introduced in the Universities of India and Ceylon, almost all the marine animals for dissection were obtained from Europe and the dogfish *Scyliorhinus* as the type of Elasmobranchs was imported in large numbers from England. With the establishment of fisheries stations in India, the universities obtained their supply of marine animals from these places and the Indian shark *Scoliodon* has been used for class-room study instead of the European dogfish. It was, therefore, necessary to have a suitable description of *Scoliodon* which differed from *Scyliorhinus* in many points. Professor K. N. Bahl asked me to work out the anatomy of this shark and write a monograph to be published in his series of Indian Zoological Memoirs.

This Memoir was first published in 1928 and was accepted by the Columbia University, New York, as partial fulfilment for my Ph. D. Degree from that University. A second Edition was issued in 1938, a third in 1950, and a fourth in 1952. In the fourth edition the text was carefully revised to provide a physiological basis for all the anatomical structures. The classification of Elasmobranchs by Moy-Thomas was adopted and the Bibliography was brought up-to-date. Modern views on the freshwater origin of fishes, on cartilage as an Embryonic adaptation, on the urea content of the Elasmobranch blood, on the functions of the Central and Autonomic Nervous System and on the thermo-receptive function of Lorenzini's ampullae have been incorporated.

My grateful acknowledgements are due to Professor K. N. Bahl, my former teacher and colleague, who guided and criticised the work in every step of the way and without whose help this work would not have been possible. He was responsible for the revision and improvements of this Memoir in all the subsequent editions.

I thank Rev. W. W. Bell, Agent, Lucknow Publishing House, for the kind interest he has taken to reprint this memoir for future circulation.

DR. (MISS) E. M. THILLAYAMPALAM,
Principal.

October 14, 1957.

Isabella Thoburn College, Lucknow, U. P.

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CHAPTER I

INTRODUCTION

Fishes occupy a unique place in the animal kingdom, since they are the forerunners of all the higher forms of life, and all the essential characters of higher vertebrates make their first appearance among them. They are as markedly successful as birds in the mastery of the medium in which they live and far outnumber all other classes of vertebrates in individuals and species. This is not to be wondered at when we remember that the sea covers about three-fourths of the surface of the globe, and that the fresh-waters of the land, the rivers and lakes, abound in fishes. More than 20,000 different species of fish are in existence at the present day and several new species are being discovered every year. Moreover, geological record testifies to the fact that fishes have flourished for nearly 400 million years and that they formed a very important section of the fauna of the Palaeozoic period.

The sub-phylum Vertebrata (Craniata) comprises two divisions: (1) the *Agnatha*, characterised by the absence of true jaws and the possession of pouch-like gills, and including such forms as the extinct *Cephalaspis* and *Pteraspis* (*Ostracodermi*) and the recent lampreys and hags, and (2) the *Gnathostomata*, possessing distinct jaws placed transversely to the length of the body and including the groups Pisces, Amphibia, Reptilia, Aves and Mammalia. Of these five groups of the *Gnathostomata*, the Pisces are the lowest and are distinguished by the presence of median and paired fins supported by fin-rays and by the fact that they breathe throughout life by means of gills borne on visceral arches.

The Pisces are divided into three classes: (1) the plated-skinned fishes or *Aphetohyoidea* (*Placodermi*) including extinct forms like *Acanthodes*, *Climatius*, *Coccosteus*, *Bothriolepis*, *Macropetalichthys*, *Gemuendina*, *Palaeospondylus*, etc., (2) the cartilaginous fish or *Chondrichthyes* including sharks and dogfishes, skates and rays and the chimaeras, and (3) the bony fish or *Osteichthyes* including all the familiar marine and freshwater bony fishes.

DISTINGUISHING CHARACTERS OF THE THREE
CLASSES OF PISCES

Endoskeleton bony; exoskeleton of bony shields, plates or scales; spines generally present; hyoidean gill-slit complete and not reduced to a spiracle; hyomandibula free and not forming the suspensorium of the jaws; a well-formed operculum attached to the palatoquadrate and mandible.

1. *Aphetohyoidea*.

Endoskeleton cartilaginous, often calcified; exoskeleton of dermal denticles structurally identical with teeth; spines primitively absent; membrane-bones absent; Meckel's cartilage the principal element of lower jaw; branchial arches 5-7; gill-openings separate, without opercula (except in Holocephali); paired nasal organs, each with one external opening; no air-bladder; modern forms with myxipterygia (claspers) in the male and generally with internal fertilization.

2. *Chondrichthyes*.

Endoskeleton typically replaced by bone; exoskeleton of bony plates or scales, not structurally identical with teeth; spines primitively absent; membrane-bones dominant; primary lower jaw sheathed with membrane-bones; branchial arches 5-4½ or less; gill-openings covered by operculum; paired nasal organs, each with two external openings; air-bladder typically present; no myxipterygia in males; external fertilization typical.

3. *Osteichthyes*.

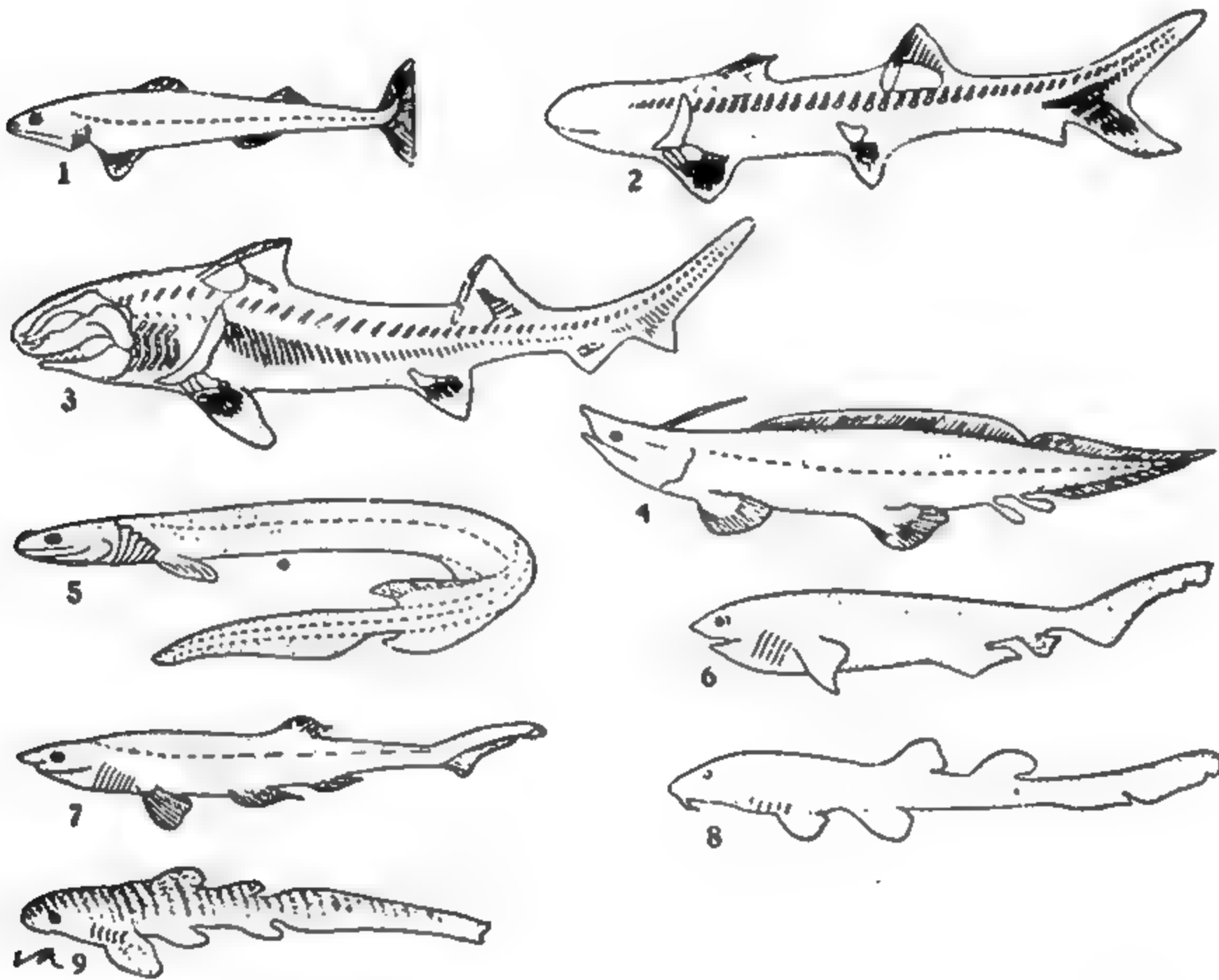
Till recently it was generally assumed that the absence of bone in the Chondrichthyes was a primitive condition and that sharks and rays represented an evolutionary stage antecedent to that of bony fishes. But recent palaeontological evidence, so ably marshalled by Romer¹, strongly suggests that bone was a primitive adult skeletal material as found in the Silurian and Devonian Agnatha and Aphetohyoidea, and that cartilage is essentially an embryonic adaptation which appears in the adult Chondrichthyes as a result of degenerative processes. The sharks should, therefore, be regarded as degenerate rather than primitive in their skeletal characters. Adult cartilage is an indication of neoteny.

¹ Romer, A. S.—Cartilage an embryonic adaptation, *American Naturalist*, vol. 76, 1942.

The class *Chondrichthyes* (*Elasmobranchii*) has been classified by Moy-Thomas¹ as follows:

Suspension of jaws amphistylic or hyostylic; teeth replace one another moderately quickly and have an outer layer of enamel-like substance beneath which lies a layer of orthodontine with numerous fine canaliculi surrounding a core of osteodontine; no operculum, gill-slits always opening directly to the outside.

Division 1 *Selachii*.



- Fig. 1—Order Pleuropterygii: *Cladoselache*. After Dean.
 Fig. 2—Order Pleuropterygii: *Ctenacanthus costellatus*. (After Moy-Thomas).
 Fig. 3—Order Protoselachii: *Hybodus hauffianus*. (After Moy-Thomas).
 Fig. 4—Order Pleuracanthodii: *Pleuracanthus*.
 Fig. 5—Family Chlamydoselachidae: *Chlamydoselachus anguineus*.
 Fig. 6—Family Hexepranchidae: *Hexanchus corinus*. (The number of gill-slits is six and not five as shown in the figure).
 Fig. 7—Family Hexepranchidae: *Heptranchias perlo*.
 Fig. 8—Family Orectolobidae: *Chiloscyllium indicum*.
 Fig. 9—Family Orectolobidae: *Stegostoma tigrinum*.

¹ Moy-Thomas, J. A.—The early evolution and relationships of the elasmobranchs, *Biological Reviews*, January 1939.

Suspension of jaws autosystylic (holostylic); teeth replace one another in slow succession and are crushing, suggesting a molluscan diet, and have an outer enamel-like layer, the crown of the tooth being formed of numerous vertical parallel tubes of dentine; operculum covering the gill-slits present. This division includes several sub-orders with extinct genera and recent forms like *Chimaera*, *Callorhynchus* and *Harriotta* forming the sub-order Holocephali.

Division 2 Bradyodonti.

The Selachii are divided into four orders:

Order 1. *Pleuropterygii*.

Earliest extinct elasmobranchs in which the dermal armour has become reduced to a covering of minute denticles and the dorsal fin-spines; two dorsal fins, each with basals and radials consisting of parallel rods of cartilage; paired fins forming triangular flaps of the body wall, with a skeleton of parallel bars of cartilage; typical shark-like jaws with 'cladodont' teeth (with a large central cusp and a varying number of smaller lateral ones); no claspers.

Examples: *Cladoselache* (fig. 1, Upper Devonian), *Ctenacanthus* (fig. 2, Lower Carboniferous).

Order 2. *Protoselachii*.

Extinct elasmobranchs in which the pectoral fins are no longer fin-folds, but have become notched at their posterior margins; claspers present.

Examples: *Hybodus* (fig. 3, Lower Jurassic), *Trityschius*, (Lower Carboniferous).

Order 3. *Pleuracanthodii* (*Ichthyotomi*).

Extinct sharks with biserially 'archipterygial' pectoral fins, diphyccercal tail; elongated dorsal fins, divided anal fin and a cephalic spine at the posterior end of the head; jaw-suspension amphistylic and teeth of the "diplodus" type (with two prominent lateral cusps and a single median smaller one).

Example: *Pleuracanthus* (fig. 4, Lower Permian).

Order 4. *Euselachii*.

Extinct and all the *living* elasmobranchs, having their skin covered with placoid scales, there being no dermal plates or true scales, although spines are present in front of fins in the most primitive types and in a few living genera; fins with constricted bases, the pectorals having three basal pieces from which preaxial radials spread out; constricted notochord; centra of chordal origin; jaws

primitively amphistylic, but hyostylic in most modern forms with a large hyomandibula; two halves of pelvic girdle fused together; epibranchial arteries corresponding to the branchial slits; a rectal gland.

Examples: All living elasmobranchs (figs. 5-42).

The order Euselachii¹ is divided into *five* sub-orders as follows:

Sub-order 1. *Notidani*.

One dorsal fin without spines; a ventral fin; gill-openings 5-7; sixth gill-arch complete; suspensorium amphistylic; single rostral cartilage; notochord unconstricted anteriorly; vertebrae diplospondylic; centra undifferentiated anteriorly but tectospondylic posteriorly.

Examples: *Chlamydoselachus* (fig. 5, Pacific and Atlantic); *Hexanchus* (fig. 6, Warm and Tropical seas); *Heptranchias* (fig. 7, Atlantic and Mediterranean).

Sub-order 2. *Heterodonti*.

Two dorsal fins with spines; a ventral fin; gill-openings 5; sixth gill-arch absent; suspensorium amphistylic to hyostylic; rostral cartilages absent; notochord constricted; vertebrae monospondylic; centra tectospondylic.

Examples: *Heterodontus* (*Cestracion*) (fig. 35, Pacific); *Palaeospinax* (Jurassic).

Sub-order 3. *Squaloidei*.

Two dorsal fins with spines; ventral fin absent; gill-openings 5-6; sixth gill-arch absent or complete; suspensorium hyostylic; rostral cartilage single; notochord constricted; vertebrae monospondylic; centra cyclo- or tectospondylic.

Examples: *Squalus* (fig. 36, temperate seas); *Etmopterus lucifer* (fig. 37, Japan Sea); *Acanthias* (fig. 38, temperate seas); *Echinorhinus* (fig. 39, Cape Cod). *Somniosus microcephalus* (fig. 40, all cold seas); *Pristiophorus* (fig. 41, Japan and Australia); *Rhina* (angel-fish, fig. 42, tropical and temperate seas).

Sub-order 4. *Scyllioidei* (*Galeoidea*).

Two dorsal fins without spines; a ventral fin; gill-openings 5; sixth gill-arch rudimentary; suspensorium hyostylic; rostral cartilages triradiate; notochord constricted; vertebrae monospondylic; centra asterospondylic.

Sub-order 5. *Raiioidei*.

Head, body and pectorals depressed, broadened and joined to form a disc; eyes and spiracles dorsal, but nostrils, gill-openings

¹ Professor Bertin (Inst. Oceanogr, Monaco, No. 775, June 1939) has classified the Euselachii into *five* groups: Notidaniformes, Scylliformes, Musteliformes, Lamniformes and Squaliformes.

and mouth ventral; teeth in bands of pavements; tail more or less distinct from disc; mainly ovoviviparous, some oviparous.

Examples: *Pristis* (tropical and subtropical seas), *Rhinobatus* (tropical and temperate seas), *Rhynchobatus* (Indian seas), *Raja* (tropical and temperate seas), *Discobatus* (China and Japan seas), *Torpedo* (Mediterranean sea, Atlantic and Indian oceans), *Narcine*, *Asterope* and *Temera* (Indian seas), *Trygon*, *Urogymnus* and *Pteroplatea* (Indian seas).

The sub-order *Scyllioidei* (*Galeoidei*) comprises two super-families which are distinguished as follows:

Nictitating membrane absent; vertebral centra with four main uncalcified areas without calcified rods; radiating calcifications in the calcified areas, frequently branching, rarely with concentric laminae; spiral valve of the ring type.

Examples: *Chiloscyllium* (fig. 8) and *Stegostoma* (fig. 9) (Indian seas); *Ginglymostoma* (fig. 10, Warm seas); *Rhineodon* (fig. 11, tropical Pacific, Galapagos Archipelago, Florida, Lower California and Japan); *Carcharias* (*Odontaspis*) (fig. 12, Atlantic and Mediterranean); *Scapanorhynchus* (*Mitsukurina*) (fig. 13, Japan Sea); *Isurus* (fig. 14, Mediterranean, Mexico, Hawaii and Japan); *Vulpecula* (*Alopias*) (fig. 15, Warm seas); *Cetorhinus* (fig. 16, North sea and California); *Carcharodon* (Europe, New England, California, Hawaii and Japan).

.....1. Super-family ISURIDA

Nictitating membrane present or rudimentary; vertebral centra with calcified rays extending into each of the four main uncalcified areas; secondary calcifications in the form of a "Maltese cross" or rudimentary; rostral cartilages three, united; pectoral fin with well-developed propterygium and mesopterygium; caudal axis low; spiral valve of spiral or scroll type.

.....2. Super-family CARCHARINIDA

The super-family *Carcharinida* comprises seven families which are distinguished as follows:

Nictitating membrane rudimentary; vertebral centra showing all stages of development of type: oviparous; teeth small, pluricuspid, several series in function; denticles with incomplete keels.

(a) Vertebral centra cyclospondylic; anterior nasal valves not reaching the mouth.

Examples: *Pseudotriakis* (South Atlantic), *Catulus* (Atlantic and Sagami sea, Japan), etc. (figs. 17-21)

1. Family Catulidae.

(b) Vertebral centra intermediate in type.

Examples: *Caliscyllium* (Sagami sea), *Halaelurus* (Japan to East Indies), etc. (fig. 22-24).

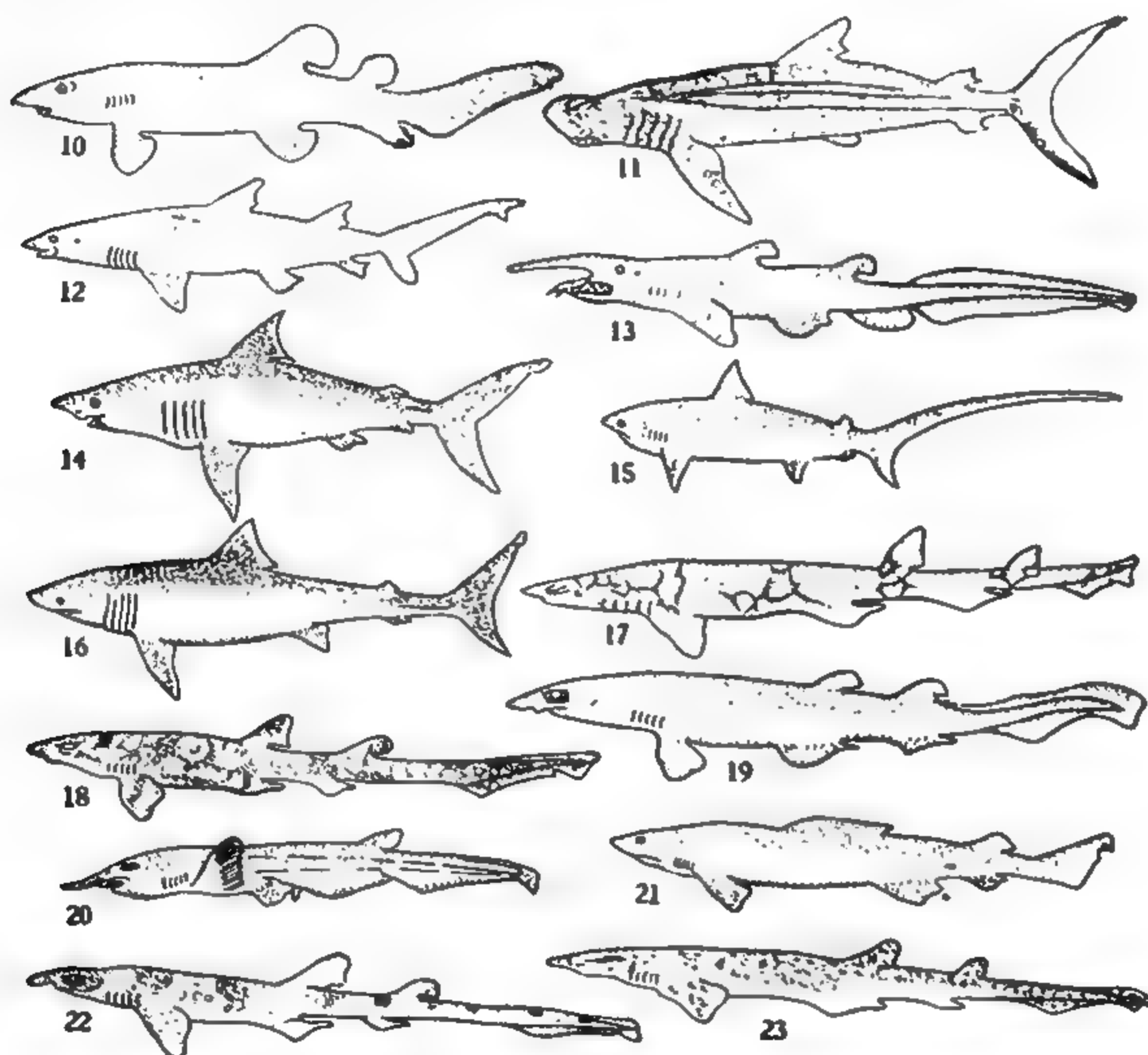
2. Family Halaeluridae.

(c) Vertebral centra of complete Maltese type.

Example: *Atelomycterus* (fig. 25, Coral reefs of the Malay Archipelago).

3. Family *Atelomycteridae*.

Nictitating membrane more or less perfectly developed; vertebral centra of complete Maltese cross type; ovoviviparous; several series of teeth in function.



- Fig. 10—Family Orectolobidae: *Ginglymostoma cirratum*.
 Fig. 11—Family Rhineodontidae: *Rhineodon typus*.
 Fig. 12—Family Carchariidae: *Carcharias taurus*.
 Fig. 13—Family Scapanorhynchidae: *Scapanorhynchus owstoni*.
 Fig. 14—Family Isuridae: *Isurus punctatus*.
 Fig. 15—Family Vulpeculidae: *Vulpecula marina*.
 Fig. 16—Family Cetorhinidae: *Cetorhinus maximus*.
 Fig. 17—Family Catulidae: *Catulus retifer*.
 Fig. 18—Family Catulidae: *Catulus torazame*.
 Fig. 19—Family Catulidae: *Parmaturus xaniurus*.
 Fig. 20—Family Catulidae: *Pentanchus profundicolus*.
 Fig. 21—Family Catulidae: *Pseudotriakis microdon*.
 Fig. 22—Family Halacluridae: *Halaclurus burgeri*.
 Fig. 23—Family Halacluridae: *Halaclurus bivius*.

Examples: *Triakis* (fig. 26, Japan), *Triaenodon* (Red sea; Indian ocean and Arabian sea), *Leptocharias* (Cabenda Bay, South Africa).

4. Family *Triakidae*.

Nictitating membrane complete; one series of teeth in function.

(a) Teeth blunt or with rudimentary cusps; anterior nasal valves short, far from mouth.

Example: *Galeorhinus*: (fig. 27, Japan, California and England).

5. Family *Galeorhinidae*.

(b) Skull not expanded laterally.

Examples: *vide infra*.

6. Family *Carcharinidae*.

(c) Skull expanded laterally across frontal region.

Example: *Sphyrna* (figs. 32-34, tropical and sub-tropical seas).

7. Family *Sphyrnidae*.

The genus *Scoliodon* which forms the subject of this memoir belongs to the family *Carcharinidae* which is the largest family of recent sharks and is characterized by the following features:

DISTINGUISHING CHARACTERS OF THE FAMILY
CARCHARINIDAE

Body elongate; head and snout depressed; tail compressed; eyes lateral, provided with a more or less perfectly developed nictitating membrane; nostrils below the snout; mouth crescent-shaped, inferior; two dorsals, not preceded by a spine, the first dorsal forward of the ventrals; a ventral median fin.

Fossil teeth representing nearly all the genera of this family are common in the Tertiary rocks.

KEY TO THE GENERA OF THE FAMILY CARCHARINIDAE

Teeth compressed, one-cusped, one series in function; a nictitating membrane; caudal pits present.

Spiracles minute

teeth not serrate, subequal in both jaws, oblique and notched.

Distribution: Indian Ocean.

1. *Loxodon*.

Spiracles absent

teeth not serrate, bases swollen, points slender, oblique.

Distribution: Bay of Bengal.

2. *Physodon*

teeth not serrate, bases swollen, cusps slender, pointed; one median tooth on upper jaw, and two on lower.

Distribution: Red Sea; Indian seas to the Malay Archipelago and beyond up to Japan.

3. *Scoliodon* (fig. 30)

teeth not serrate, narrow on broad bases, upper nearly erect, lower erect.

Distribution: Red sea; East coast of Africa; coasts of Sind; Indian Ocean up to Australia.

4. *Aprionodon*.

teeth with serrations on the base in the upper jaw only.

Distribution: Seas of India to New Guinea.

5. *Hypoprion*.

teeth serrate, some or all, on bases and cusps, first dorsal near the pectorals.

Distribution: Atlantic, Japan, fresh waters of the Ganges and Lakes Nicaragua and Pontchartrain.

6. *Carcharinus* (fig. 31).

teeth all serrate, slightly swollen, cusps oblique, first dorsal near the pelvics.

Distribution: Temperate and tropical seas.

7. *Galeus* (fig. 28).

Spiracles minute

teeth serrate on both jaws, upper teeth oblique.

Distribution: Mediterranean and Atlantic.

8. *Thalassorhinus*.

teeth serrate and oblique on both jaws, labial fold along the upper jaw; subcaudal long.

Distribution: Arctic, tropical and temperate seas.

9. *Galeocerdo* (fig. 29)

teeth serrate on the upper jaw only, labial folds on both jaws, subcaudal long.

Distribution: Coromandel coast of India to the Malay Archipelago.

10. *Hemigaleus*.

Spiracles small

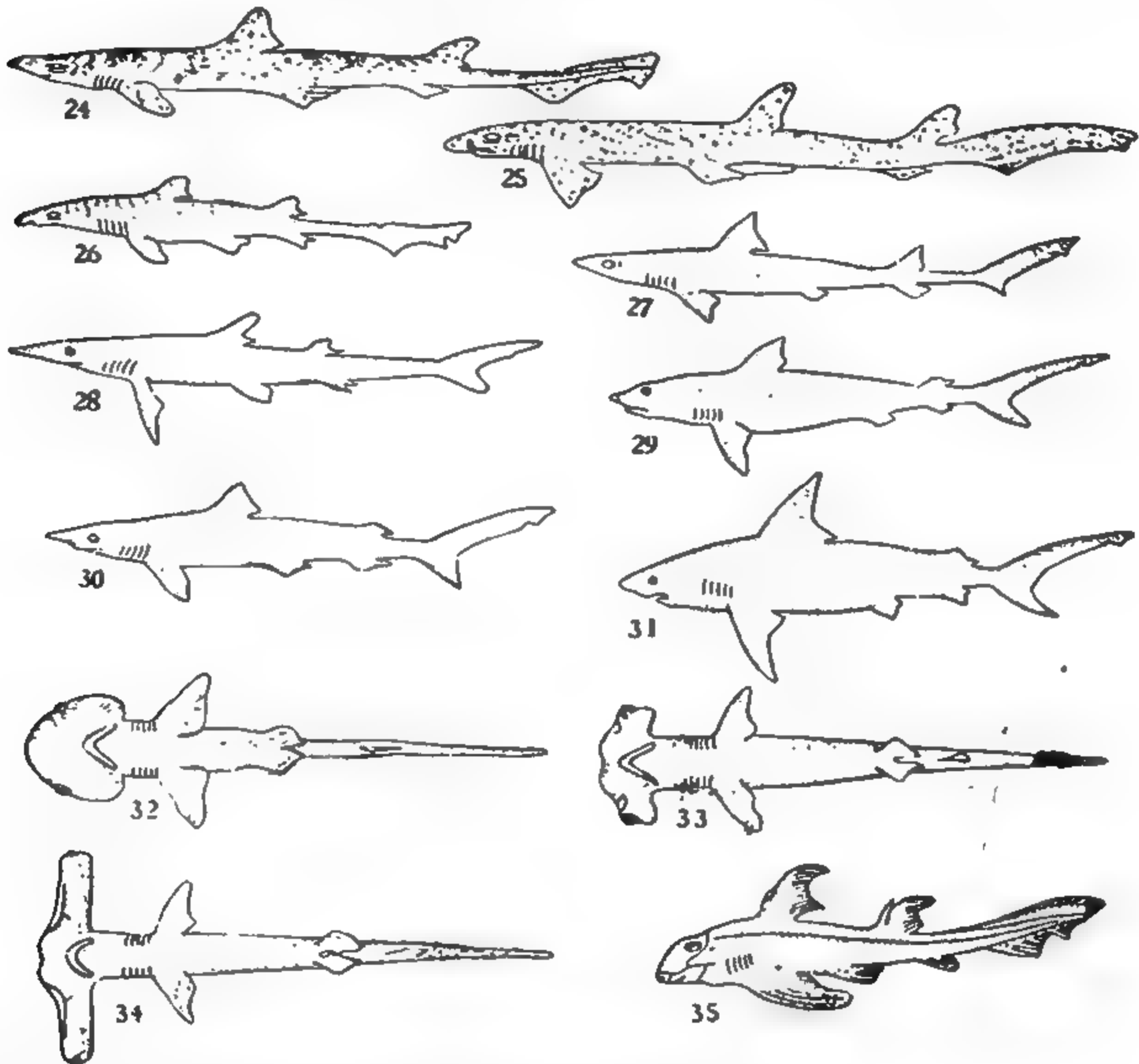
caudal pits rudimentary; subcaudal short; teeth serrate; notched, oblique; labial folds.

Distribution: Mediterranean, California and Japan.

11. *Eugaleus*.

DISTINGUISHING CHARACTERS OF THE GENUS *Scoliodon*

Body compressed; head depressed; snout elongate, blunt. Mouth inferior, greatly arched, with short labial folds at the angles. Teeth alike in the two jaws, sectorial, more or less smooth on the edges, broad based, with a triangular cusp that is inclined outward over a notch above the base on the outer edge; a median upper



- Fig. 24—Family Halaeluridae: *Calliscyllium venustum*.
 Fig. 25—Family Atelomycteridae: *Atelomycterus marmoratus*.
 Fig. 26—Family Triakidae: *Triakis scyllium*.
 Fig. 27—Family Galeorhinidae: *Galeorhinus canis*.
 Fig. 28—Family Carcharinidae: *Galeus glaucus*.
 Fig. 29—Family Carcharinidae: *Galeocerdo tigrinum*.
 Fig. 30—Family Carcharinidae: *Scoliodon walbeehmi*.
 Fig. 31—Family Carcharinidae: *Carcharias milberti*.
 Fig. 32—Family Sphyrnidae: *Sphyrna tudes*.
 Fig. 33—Family Sphyrnidae: *Sphyrna zygaena*.
 Fig. 34—Family Sphyrnidae: *Sphyrna blochii*.
 Fig. 35—Order Heterodontea, Family Heterodontidae: *Heterodontus philippi*.

tooth, and two symphyseal teeth in the lower series, smaller in some species. Nictitating membrane well developed. Caudal pits distinct; subcaudal lobe prominent. Scales minute, with three to five keels.

The genus *Scoliodon* has a very wide geographical distribution; it has been recorded from Zanzibar to Ceylon, and Ceylon to the Malay Archipelago in the Indian Ocean, from the Bay of Bengal,

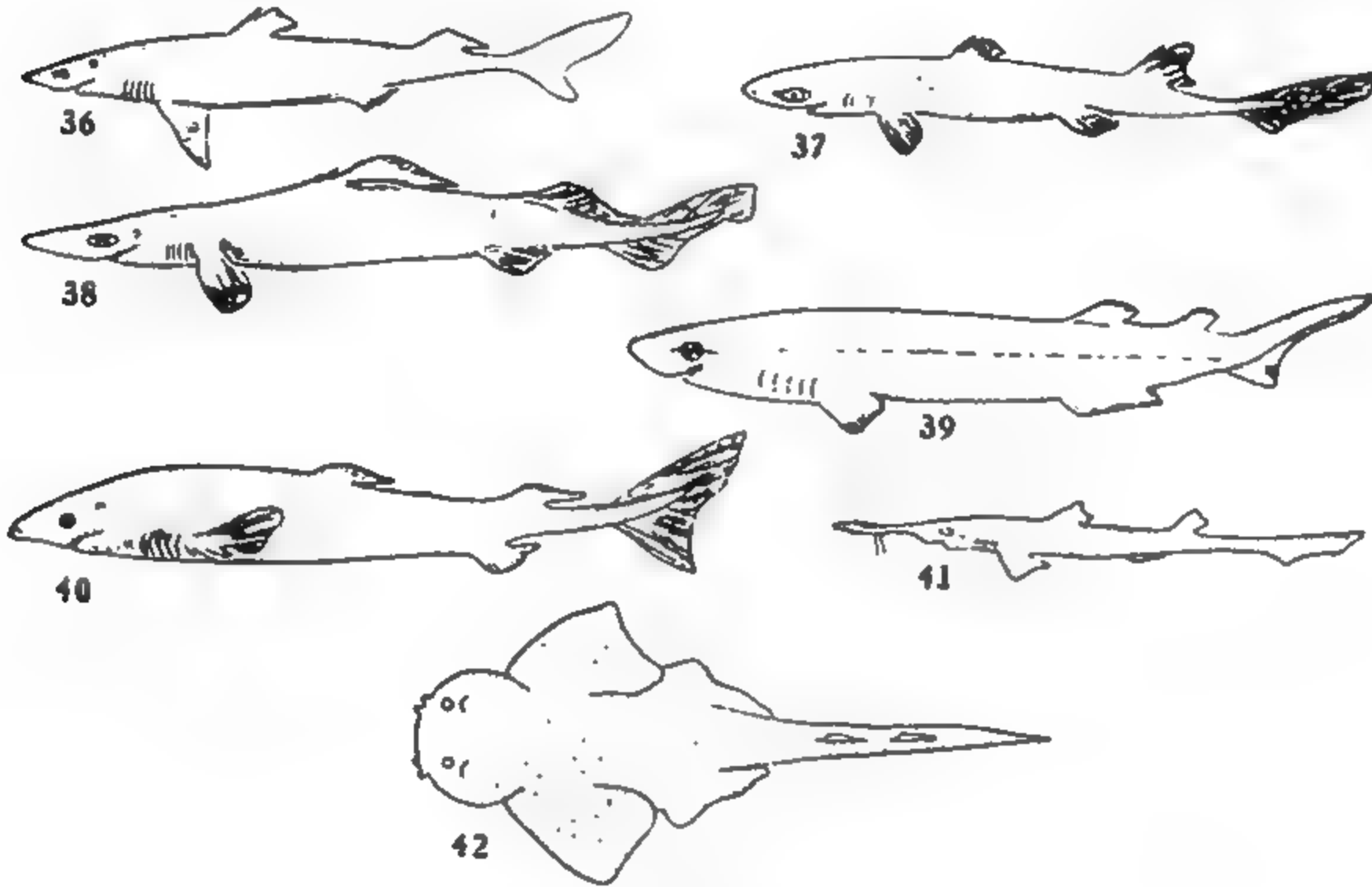


Fig. 36—Order Squalca, Family Squalidae: *Squalus acanthias*.

Fig. 37—Family Squalidae: *Etmopterus lucifer*.

Fig. 38—Family Squalidae: *Acanthias hystriocosum*.

Fig. 39—Family Echinorhinidae: *Echinorhinus brucus*.

Fig. 40—Family Scymnorhinidae: *Somniosus microcephalus*.

Fig. 41—Family Pristiophoridae: *Pristiophorus japonicus*.

Fig. 42—Family Rhinidae: *Rhina californica*.

the East Indies (Amboyna), and the Philippine Islands, from Mexico to Panama in the Eastern Pacific, from Labrador to Brazil in the Atlantic, from Cuba in West Indies, and also off the Eastern Coasts of South America; it has also been found fossil in the geological strata of the Lower Eocene and later period.

Grace White distinguishes as many as *nine* species of *Scoliodon*, of which the following *four* are common in the Indian seas:

¹ Grace White, E—(1) "A classification and phylogeny of the Elasmobranch Fishes," American Museum Novitates, April 3, 1936.

.. .. —(2) "Interrelationships of the Elasmobranchs with a Key to the Order Galca", Bulletin of the American Museum of Natural History, vol. LXXIV, December, 1937.

KEY TO THE INDIAN SPECIES OF *Scoliodon*

Base of the ventral median fin more than twice the length of that of the second dorsal.

labial folds short, on the lower jaws, not on the upper.

Distribution: Seas of India to the Malay Archipelago.

1. *S. sorrakowah*¹.

Base of the ventral median fin not more than twice the length of that of the second dorsal.

labial folds in the angles; length of snout nearly equal to the distance from the eye to the pectoral fin.

Distribution: Bay of Bengal.

2. *S. dumerilii*.

labial folds short, on the lower jaws, not on the upper.

Distribution: Red Sea, Indian Ocean and the Malay Archipelago.

3. *S. palasorrah*².

labial folds in the angles and slightly on the lower jaws; distance between outer angles of nostrils and between them and end of snout about equal; ventral median and second dorsal fins unequal, the latter posterior.

Distribution: Seas of India to the Malay Archipelago and Japan.

4. *S. walbeehmi*.

HISTORY OF THE GENUS *Scoliodon*

The genus *Scoliodon* was first instituted and described by Müller and Henle (1837), but Gill (1861) divided it into two genera, *Scoliodon* and *Aprionodon*. Francis Day³, however, in his "Fishes of India" (1878) combined *Scoliodon* with *Aprionodon*, *Physodon*, *Hypoprion* and *Prionodon* of Muller and Henle to form the genus *Carcharias*, a name originally introduced by Rafinesque in 1810 for the species *Carcharias torus*. In 1913 Samuel Garman⁴ in his memoir on the Plagiostomia, split up Day's genus *Carcharias* into several genera and restricted the name *Carcharias* to the genus as originally instituted by Rafinesque and characterized, amongst other features, by the presence of a small spiracle and by the absence of nictitating mem-

¹ Tamil *sorra*, a shark; *kowah*, black; black shark

² Tamil *palasorrah*, milk-coloured shark

³ Day, F.—The Fauna of British India: Fishes, vol. I, London, 1889.

⁴ Garman, Samuel.—The Plagiostomia: Memoirs of the Museum of Comparative Zoology at Harvard College, vol. XXXVI. 1913.

branes in its small eyes. Accordingly, about *fourteen* species assigned by Day to his genus *Carcharias* were distributed by Garman over the genera *Scoliodon*, *Loxodon*, *Physodon*, *Hypoprion*, *Aprionodon* and *Carcharinus* which were reconstituted and redefined by him to include forms possessing nictitating membranes in their eyes.

Jordan¹ (1923) and Grace White² (1937) have revised Garman's classification of Elasmobranchs in several respects but they have both retained the family Carcharinidae and the genus *Scoliodon* as defined by Garman.

¹ Jordan D.S.—A Classification of Fishes including Families and Genera as far as known. Stanford Univ. Pub., Bio. Sci., vol. III. 1922-23.

² Grace White, E.—(1) "A Classification and phylogeny of the Elasmobranch Fishes, American Museum Novitates, April 3, 1936.

.. .. —(2) "Interrelationships of the Elasmobranchs with a Key to the Order Galea", Bulletin of the American Museum of Natural History, vol., LXXIV, December 1937.

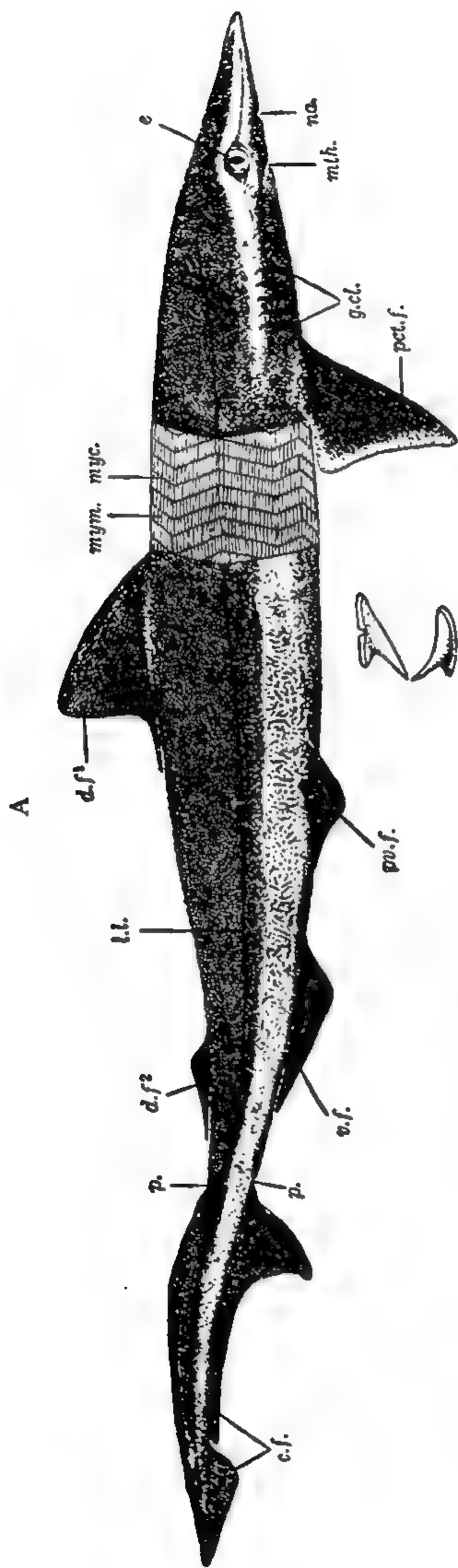
CHAPTER II

EXTERNAL CHARACTERS

The shark *Scoliodon* (fig. 43 A) has a long, laterally compressed, spindle-shaped body tapering at both ends, a full grown specimen being about two feet in length. The body is divisible into head, trunk and tail, though there are no distinct boundaries between these three regions. The head is strongly compressed dorso-ventrally and is produced in front into a wedge-shaped snout; the trunk is almost elliptical in transverse section, its thickest part lying in front of the middle of the body; the trunk gradually tapers behind into the tail which is laterally compressed and is bent upwards at a small angle. The colour of the body is dark grey above and pale white beneath, while the posterior portions of the caudal fin are more or less dark.

The shark, like most other fishes, is provided with two sets of fins which are flattened expansions of the skin supported by cartilaginous rods and horny fin-rays: these are the *median* unpaired fins and the *lateral* paired fins. The median fins comprise the two dorsals, a caudal and a ventral. The *first dorsal* is triangular in shape and is situated a little in front of the middle of the body; the *second dorsal* is also triangular in outline but is very small and is situated mid-way between the first dorsal and the tip of the tail. The *caudal fin* extends along the dorsal and ventral surfaces of the tail in the median line and forms a dorsal and a ventral lobe; the dorsal lobe is very much reduced and forms only a low ridge along the greater part of the upper surface, but the ventral lobe is well developed and is divided into two parts, the anterior part being much larger and more extensive than the posterior. At the root of the tail there is a shallow pit both on the dorsal and ventral surfaces: these are called the *caudal pits* and form a characteristic feature of this genus. The *ventral median fin*¹ is situated in the mid-ventral line about two inches in front of the caudal fin, more or less opposite the second dorsal. The basal edges of each of the two dorsals and of the ventral fin are produced behind into long and narrow fleshy processes called the *basal lobes*.

¹The ventral median fin is sometimes called the *anal fin*, but this name is not appropriate.



B

Fig. 43—A. Side view of the shark *Scoliodon sorrakowah* (female), with a part of the skin removed to show the muscles (one-third natural size). c.f., caudal fin; d.f.1, first dorsal fin; d.f.2, second dorsal fin; e., eye; g.c.l., gill-clefts; l.l., lateral line; mth., mouth; myc., myocommata; mym., myotomes; na., nasal aperture; p., pectoral fin; pv.f., median ventral fin; v.f., pelvic fin; v.f., pelvic fin; v.f., pelvic fin. B. Teeth of the upper and lower jaws.

Of the lateral fins, there are two pairs, an anterior pair called the pectorals and a posterior pair, the pelvics. The large *pectorals* originate from the ventro-lateral margins of the body immediately behind the gill-clefts and spread out more or less horizontally as triangular expansions. The *pelvics* are much smaller than the pectorals and arise close together from the ventral surface at the junction of the trunk and tail, and enclose the *cloacal aperture* between them. In the female, these fins are simple sub-triangular appendages, but in the male each of them has a copulatory organ called the *clasper* or *myxipterygium* connected with its inner edge. Each clasper is a stiff rod-like appendage having a groove on its dorsal surface which leads into a cavity, the *siphon*, beginning at the base of the clasper (Chapter XI). All the fins are directed backward, a feature which is of advantage in forward progression.

The *mouth* is wide crescentic opening situated on the ventral side of the head owing to the forward prolongation of the snout. It is bounded by the upper and lower jaws, each of which is armed with one or two rows of backwardly directed teeth, having smooth non-serrated edges (fig. 43 B). In catching its prey the shark brings its jaws into play by raising the snout and thrusting the mouth forward.

The large circular eyes are situated at the sides of the head. The upper and lower eyelids are merely outgrowths of the skin of the head and are movable; further, each eye is provided with a movable *nictitating membrane*¹ which lies along the antero-ventral border and can be drawn over the eye in time of danger. The pupil is narrow and vertical. The olfactory organs open to the exterior by means of two obliquely placed crescentic apertures, the *nostrils*², one on each side, angle of the mouth. A small fold of skin from the anterior edge partially covers each nostril. In the shark, as in most other fishes, the nostrils are only olfactory and have no respiratory function; they have no connection with the mouth, there being no internal nostrils. Behind the eyes are situated a series of vertical slits, *five* on each side, called the *branchial* or gill-



Fig. 44—The left eye. *i.*, integument; *n. m.*, nictitating membrane; *p.*, pupil.

¹ A complete nictitating membrane is found only in the Carcharinidae and Sphyrnidae, which are the most specialized of the pelagic types of Elasmobranchs.

² In *Scyliorhinus* and allied types the nasal openings communicate by wide nasoral grooves with the mouth, but these grooves are absent in *Scoliodon*.

clefts; these apertures lead into the gill-pouches and thence into the pharynx.

In the allied genera *Loxodon*, *Galeocerdo* and *Hemigaleus*, there is a minute opening, the *spiracle*, in front of the gill-slits, but this opening is absent in *Scoliodon*.

The *cloacal aperture* is an elongated opening at the root of the tail between the two pelvic fins; it leads into the *cloaca* or the common chamber into which the intestine and the urinary and genital ducts open. There is a pair of openings situated on elevated papillae on either side of the cloaca; these are the *abdominal pores*, through which the coelom communicates with the exterior.

A faint line runs on either side of the body extending from the head to the posterior end of the tail: this is called the *lateral line* and marks the position of an underlying canal which runs along each side of the body and contains special receptor organs (Chapter X). The lateral-line canal extends anteriorly on to the head where it branches into several canals; at intervals these canals open to the exterior through minute pores. Besides these pores of the lateral line canals, there are numerous groups of small openings on the head and snout: these are the *ampullary pores* (fig. 81).

The shark is an inhabitant of the open sea and depends on its swift movements in water for the capture of its prey and flight from its enemies. It therefore possesses a perfectly streamlined body with a flattened pointed snout and a tapering tail to enable it to swim swiftly in water. From a mechanical point of view the body is perfectly adapted for cleaving the water, there being no rigid projections or sharp angles in the contour of the body.

CHAPTER III

THE SKIN AND EXOSKELETON

The skin or *integument* consists of two layers: (a) an outer *epidermis* composed of many layers of epithelial cells amongst which are interspersed numerous unicellular *mucous glands*, and (b) an inner *dermis* consisting of dense connective tissue mingled with smooth muscle-fibres, blood-capillaries, pigment cells and nerves. The dermis is firmly attached to the underlying muscles and consequently the skin fits very closely over the whole body, and is removed with some difficulty. In a fresh specimen the skin is slimy, but in preserved specimens the slimy mucus is generally removed and the skin feels rough. This roughness of the skin is due to the presence of closely lying minute dermal denticles called *odontoids* or *placoid scales*, which are arranged in regular oblique rows and form the exoskeleton of the shark covering the entire surface of the body and even parts of the fins.

A typical placoid scale (fig. 45) consists of a diamond-shaped *basal plate* imbedded in the skin to enclose an underlying pulp-cavity, and a flat trident *spine* projecting out of the skin. As the spines of the scales are directed backward, the skin feels rougher when a finger is passed over it forward than backward. The surface of the spine is not smooth but presents a stratified appearance under the microscope. Strong fibres of connective tissue attached to the basal plate anchor the scale within the integument, while a perforation at the base of the spine leads from the pulp-cavity into a canal traversing the middle of the spine. During life this pulp-cavity is filled with vascular connective tissue called the *pulp* containing numerous *odontoblasts* or dentine-forming cells, blood-vessels, nerves and lymph-channels. The basal plate is formed of a trabecular calcified tissue, closely allied to the *cement* of our teeth, while the spine is composed of a hard calcareous substance traversed by minute, nearly parallel, canaliculi with delicate branches, called the *dentine*, which is coated externally with a hard dense substance, the *enamel*. The placoid scales are derived partly from the dermis and partly from the epidermis; the basal plate and the dentine of the spine are derived from mesoderm, while the enamel is secreted by the ectoderm. Both in

in structure and development, the placoid scales are closely comparable to the teeth, the latter being merely specialized placoid scales.

The placoid scales represent a very primitive form of scale; they have been found in the earliest known fossil Elasmobranchs and are distinctive of all Elasmobranchs living at the present time.

The skin of the shark is primarily a protective wrapper: the placoid scales are protective integumentary modifications, while the

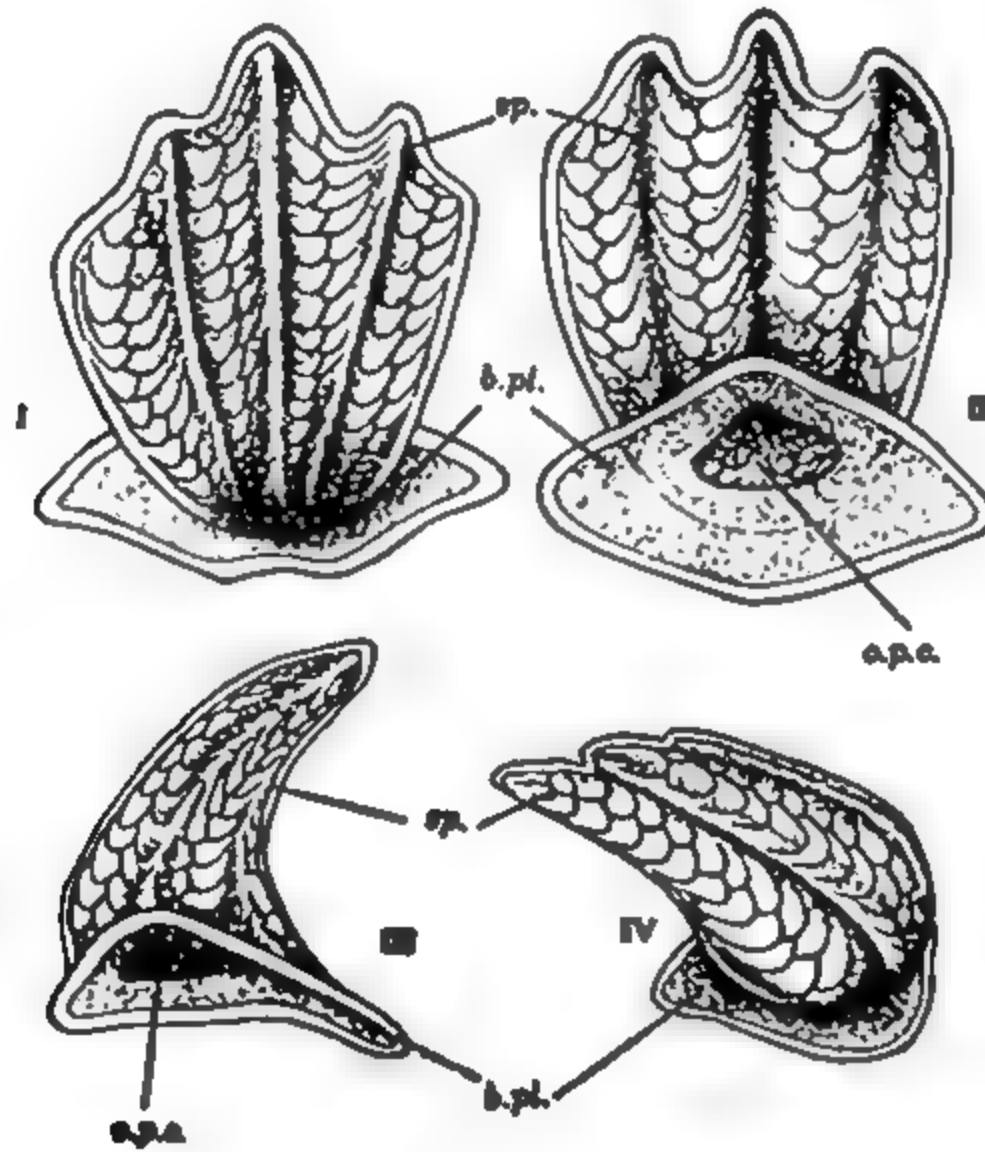


Fig 45—Dermal denticles (placoid scales) of *Scoliodon*. I.. dorsal view. II. ventral view. III. ventro-lateral view; IV. dorso-lateral view. b. pl., basal plate; o.p.c., opening of the pulp-cavity; sp., spine (\times cir. 135)

slimy secretion of the skin minimizes friction as the shark glides along in water and also forms a protective coating to resist the entrance of bacteria and fungi.

The cured skin of sharks, commercially known as *shagreen*, is used for smoothing and polishing furniture and also for making covers for handles to assist in gripping.

CHAPTER IV THE ENDOSKELETON

The endoskeleton is composed entirely of cartilage hardened at places by calcifications, there being no true bone. It can be divided into: (a) the *axial skeleton*, consisting of the vertebral column and skull, and (b) the *appendicular skeleton* including the pectoral and pelvic girdles and the skeletal elements of the fins.

(a) THE AXIAL SKELETON

The *vertebral column* is a chain of cartilaginous structures, the *vertebrae*, which are developed around an elastic axis of vacuolated cells, the *notochord*. In its early stages the notochord is enclosed in a thin covering membrane called the *primary sheath*, but later this primary sheath is strengthened by a thick internal fibrous sheath known as the *secondary* or *chordal sheath* formed by the transformation of the peripheral cells of the notochord itself. Four paired pieces of cartilage, called the dorsal and ventral *arcualia*, are laid in the tissue surrounding the notochord in each segment; the anterior smaller arcualia grow upward to form the interneural plates, while the posterior larger arcualia form the neural plates and transverse processes and surround the notochord and also invade its secondary sheath. On invasion by the cartilage, the chordal sheath becomes differentiated into alternate fibrous and cartilaginous regions; the cartilaginous regions form the vertebral bodies or *centra*, while the small fibrous regions give rise to the *intervertebral ligaments*.

Vertebrae with centra formed entirely or mainly within the chordal sheath, as in *Scoliodon*, are known as *chordo-centrous*. In Teleostei and Ganoidei, the chordal sheath is inconspicuous and the centra are formed only around the notochord in the connective tissue outside the primary sheath: such vertebrae are called *arci-centrous*.

The individual vertebrae vary but slightly along the length of the column and therefore a vertebra from the trunk region may be taken as a type. A trunk vertebra (fig. 46) consists of a *centrum* surrounding the slender notochord, a dorsal *neural arch* enclosing the spinal cord, and a pair of *transverse processes* projecting ventro-laterally from each centrum. The centra are short cylindrical bodies hollowed out into deep concavities at their two ends, the surface at

each end, anterior and posterior, looking very much like a watch-glass; the vertebrae are, therefore, described as *amphicoelous*. The notochord is very much constricted within the centrum, but is greatly dilated in the intervertebral spaces formed by the apposition of adjoining centra, thus presenting a moniliform or beaded appearance in a sagittal section (fig. 46 A). The centra are reinforced by calcified

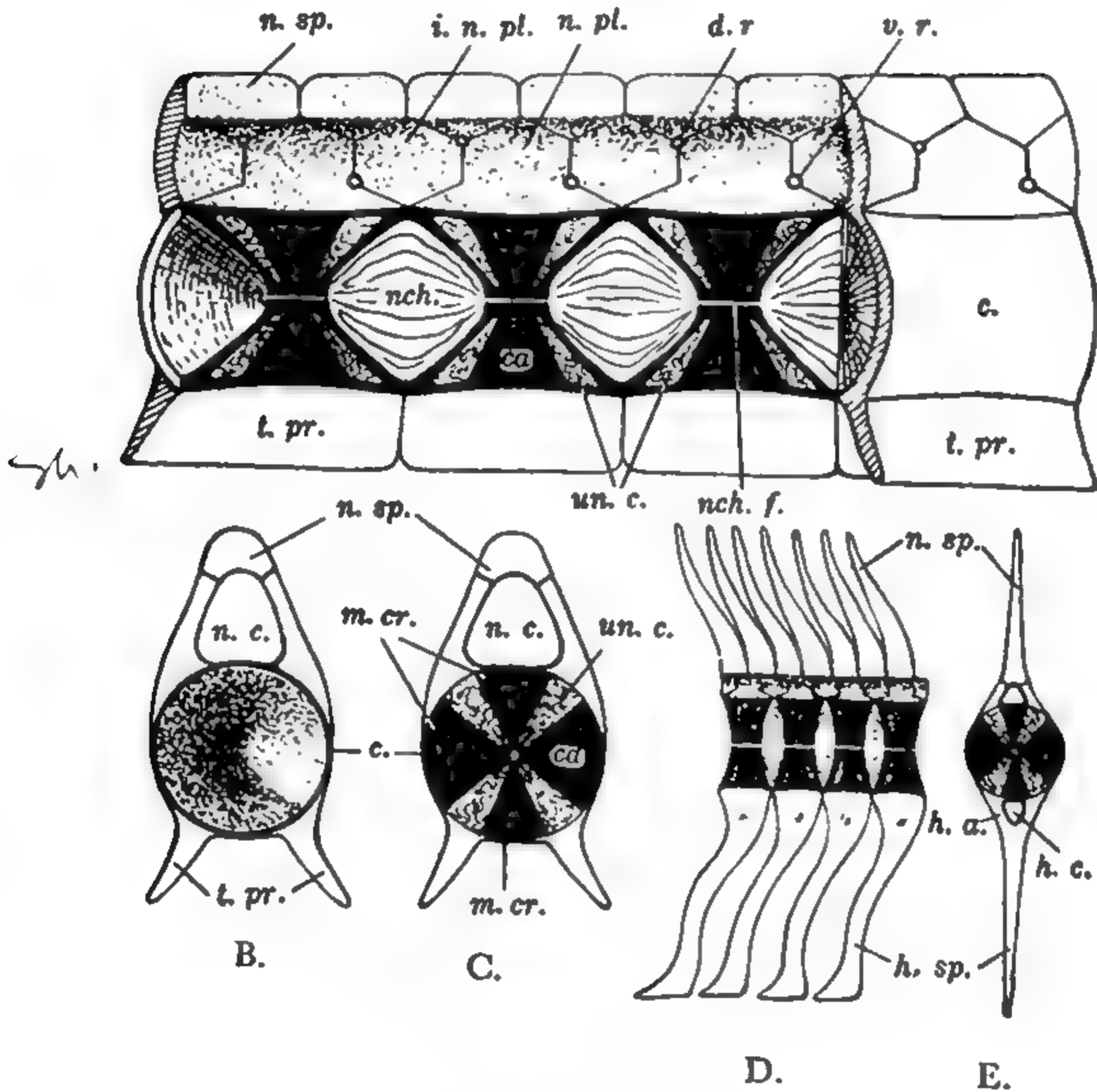


Fig. 46—A. A portion of the vertebral column of the trunk, the greater part of which is cut longitudinally; B. Front view of a trunk vertebra; C. A transverse section of the same through the middle of the centrum; D. A longitudinal section of four caudal vertebrae; E. A transverse section of a caudal vertebra through the middle of its centrum. *c.*, centrum; *ca.*, calcified portion of the centrum forming a Maltese cross *m.cr.*; *d.r.*, foramen for the dorsal nerve-root; *h.a.*, haemal arch; *h.c.*, haemal canal; *h.sp.*, haemal spine; *i.n.*, intervertebral neural plate; *n.c.*, neural canal; *nch.*, notochord; *nch.f.*, notochordal filament within the centrum; *n.pl.*, vertebral neural plate; *n.sp.*, neural spine; *t.pr.*, transverse process; *un.c.*, four uncalcified regions of centrum; *v.r.*, foramen for the ventral nerve-root. (A. $\times 2\frac{1}{2}$; B.C.D. and E. $\times 1\frac{1}{2}$).

fibro-cartilage developed as four wedges, which traverse the body of the centrum from its periphery almost to the centre, thus giving rise to a cruciform figure like a "Maltese cross"; such centra in which the secondary calcifications leave four main uncalcified areas are called *asterospondylous*. In *Scoliodon*, as in all other members of the family Carcharinidae, there are four additional stiff calcified rods extending from the centre into the four uncalcified areas (fig. 46 C).

Centra in which the calcareous matter is confined to the two cones on the two concavities are called *cyclospondylous*. If there are additional concentric calcareous rings outside the double cone, the centra are known as *lectospondylous*.

In the trunk there is always one vertebra to each myotome (except in *Hexancha*); such vertebrae are described as *monospondylic*; but in the caudal region, there are twice as many vertebrae as myotomes; such vertebrae are called *diplospondylic*.

The side of each neural arch is formed by a *vertebral neural plate* which projects upward from the dorsal surface of the centrum on each side; the spaces between successive vertebral neural plates are filled in by *intervertebral neural plates*, while the arch is completed above by *neural spines* which fill in the spaces between the upper ends of the vertebral and intervertebral neural plates. The roots of the spinal nerves make their exit through minute foramina in the neural arch; the dorsal root passes through a foramen at the upper margin of the neural plate, while the ventral root passes through a foramen at the lower margin of the intervertebral plate (fig. 46 A).

The transverse processes of the anterior vertebrae are short and extend outward, but in the posterior trunk vertebrae they bend downward and enclose an open groove, which in the caudal region is closed up to form the *haemal canal* containing the caudal artery and vein (fig. 46 E). Each haemal arch enclosing the haemal canal is produced into a backwardly directed and flattened *haemal spine* for the support of the ventral lobe of the caudal fin. The dorsal lobe of the caudal fin is likewise supported by the prolongations of the neural spines (fig. 46 D). The posterior part of the vertebral column is bent dorsally to form an asymmetrical or *heterocercal* tail (fig. 46 A).

When the vertebral column is continued straight to the termination of the tail, with the dorsal and ventral lobes of the fin symmetrically placed, as in the Dipnoi, the tail is said to be *diphycercal*. In the Teleostei, the larval tail-fin is heterocercal and the notochord is bent upward and passes into the upper lobe of the tail-

¹In the older specimens of *Scoliodon*, additional radiations of calcified tissue may occur between the four wedges described above; in *Hemiscyllium* there are always eight such radiating lamellae.

fin, as in adult *Scoliodon*; but as development proceeds, the upper lobe shrinks and disappears whilst the ventral lobe increases in size and becomes divided into two symmetrical lobes: such a secondarily formed symmetrical tail-fin is called *homocercal*.

The vertebral column forms the axial scaffolding of the body and serves as a foothold for the insertion of all the body and tail-muscles concerned in locomotion. The segmentation increases the flexibility of the column but the vertebrae are so closely bound to one another by strong fibrous connective tissue that there is little freedom of movement for individual vertebrae. In fishes flexion of the column as a whole is all that is necessary for the prevailing lateral movements of the body.

The *skull* (figs. 47-51) consists of: (1) the *cranium* surrounding and protecting the brain, (2) the *sense-capsules* enclosing the olfactory and auditory organs, and (3) the *visceral skeleton* forming the jaws and the skeletal supports of the pharynx and gills.

The *cranium* (figs. 47 and 48) is a simple cartilaginous casket with which two pairs of sense-capsules, the olfactory and the auditory, are intimately fused. The general shape of the cranium is very much like that of a violin-box, open in front and behind, with an arched roof and a flattened floor. In the hinder region the massive auditory capsules project on either side, the middle region is hollowed out on each side into a deep concavity for lodging the eyeball and its muscles and nerves, while the anterior region, besides presenting a swelling on each side formed by the olfactory capsule, gives off anteriorly three cartilages, which are prolonged forward and unite to form the *rostrum*. The cranium may be roughly divided into four regions: (a) the occipital, (b) the auditory, (c) the orbital, and (d) the ethmoidal.

The *occipital region* forms the posterior part of the cranium and is perforated behind by a large median opening, the *foramen magnum*, through which the brain is continued into the spinal cord. Immediately below this foramen there is a cup-shaped concavity which encloses the notochord and is firmly apposed to a similar concavity of the first vertebra. On either side of the foramen magnum, there is a prominent *occipital condyle* for articulation with the first vertebra. Above the foramen magnum the roof of the occipital region carries a prominent median ridge called the *occipital crest*, while external to the occipital condyle, on either side, lies a large foramen for the exit of the *tenth* or *vagus* nerve.

The *auditory region* comprises the auditory capsules and part of the cranium with which they are intimately fused. The capsules are separate from the cranium in the embryo but become firmly

united with it in the adult. On the roof of the cranium, between the two capsules (fig. 47), there is a marked oval depression, the *parietal fossa*, with a pair of apertures on each side of its posterior part: the posterior pair are the *fenestrae* or openings of the *perilymphatic spaces* of the two capsules, while through the anterior pair the *endolymphatic duct* (*aqueductus vestibuli*) of each internal ear pierces the skull. On either side of the parietal fossa is seen a low ridge marking the position of the *anterior vertical semi-circular canal* of the internal ear; a similar ridge behind the fossa marks the position of the *posterior vertical semi-circular canal*, while a prominence on the outer side of each capsule marks the position of the *horizontal semi-circular canal*. Behind and below the last ridge lies a large foramen for the exit of the *ninth* or *glosso-pharyngeal nerve*. In front of this foramen lies the oblique *post-orbital groove* which lodges the vein connecting the orbital sinus with the anterior cardinal sinus. The *articular surface for the hyomandibular cartilage* lies just below the post-orbital groove.

The *orbit* (fig. 49) lodges the eye-ball and its muscles, the large orbital blood-sinus, and a large number of nerves. The *supra-orbital ridge* marks the boundary between the roof of the cranium and the orbit. From the roof of each olfactory capsule, just in front of the orbit, arises a slender cartilage which curves backward and partially encircles the orbit: this is the *pre-orbital cartilage*. A similar cartilage, the *post-orbital cartilage*, arises from the side of each auditory capsule and curves forward along the upper border of the orbit. A lateral outgrowth of the floor of the orbit forms the *suborbital ridge* which is produced anteriorly into the *antorbital process*, forming a place for the insertion of ligaments of the upper jaw. At the upper border of the orbit (fig. 49), close to the auditory capsule, there is a large foramen through which the *superficial ophthalmics of the fifth and seventh nerves* enter the orbit; immediately below it lies the foramen for the exit of *third nerve*, and close behind it lies the foramen for the exit of the *ophthalmicus profundus branch of the fifth nerve*. At the postero-ventral angle of the orbit lies a large oval opening for the *main branches of the fifth and seventh nerves*. The *foramen for the exit of the sixth nerve* lies behind this large aperture and is separated from it by a ligament. In front of the large aperture for the fifth and seventh lie two other small apertures: the posterior is the *aperture for the inter-orbital canal* which connects the orbital sinuses of the two sides, while the anterior opening provides entrance for the *spiracular epibranchial artery* into the cranium. The large *optic foramen* for the exit of the *optic nerve* is situated in the middle of the ventral part of the orbit. Vertically above the optic foramen lies a small *opening for the exit of*

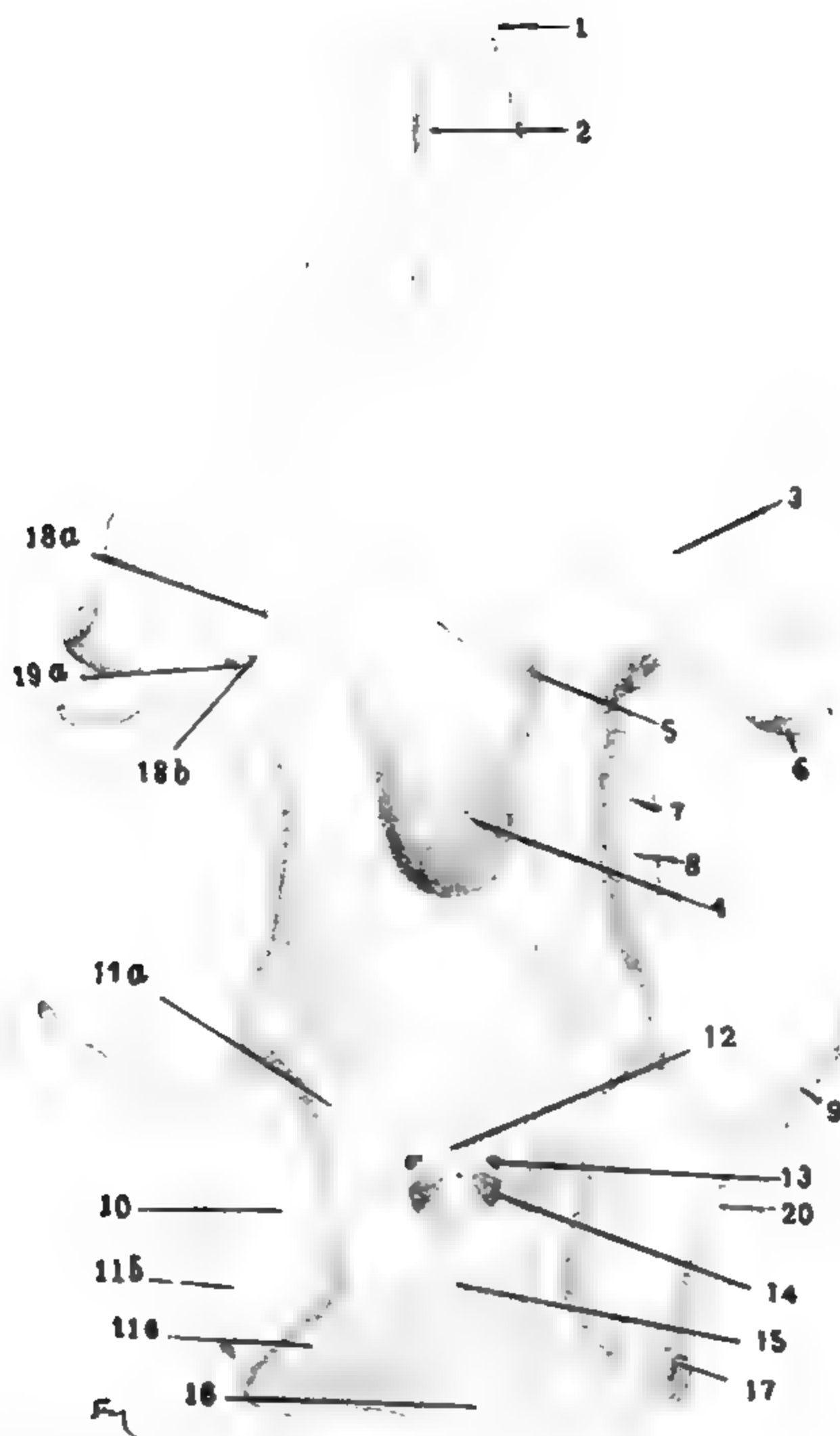


Fig. 47—Dorsal view of the skull. 1, dorso-lateral cartilage of rostrum; 2, ventro-median cartilage; 3, olfactory capsule; 4, anterior fontanelle; 5, foramen lodging the olfactory lobe; 6, pre-orbital cartilage; 7, ant-orbital process; 8, floor of the orbit (sub-orbital ridge); 9, post-orbital cartilage; 10, auditory region; 11a, 11b, 11c, ridges of anterior vertical, horizontal, and posterior vertical semi-circular canals respectively; 12, parietal fossa; 13, opening of the endolymphatic duct; 14, fenestrae; 15, occipital crest; 16, foramen magnum; 17, foramen for the *ninth* nerve; 18a and 18b, foramina for the ophthalmicus profundus nerve; 19a, posterior opening of the orbito-nasal canal; 20, articular surface for the hyomandibula. (\times cir. 2).

the fourth nerve; in front of this opening at the anterior border of the orbit, there is another small opening through which the *ophthalmicus profundus* of the fifth nerve leaves the orbit. The *posterior opening of the orbito-nasal canal*, through which the olfactory sinus communicates with the orbital sinus, is also situated at the anterior border of the orbit.

The floor of the cranium (fig. 48) is broad and flat and bears towards its hind end two obliquely transverse grooves called the *carotid canals*, one on each side; each of these canals in its anterior half bears two apertures, one leading into the cranium and the other into the orbit; the former transmits the *internal carotid artery* and the latter the *stapedial artery*. The floor of the cranium becomes narrower at its anterior end where the olfactory capsules are attached. Immediately behind the olfactory capsules lie two large prominent articular surfaces for the attachment of the *ethmo-palatine ligaments* of the upper jaw, while in front of these articular surfaces lie the *anterior openings of the orbito-nasal canals*.

The *ethmoidal region* includes the anterior region of the cranium, the olfactory capsules and the rostrum. Like the auditory capsules, the olfactory capsules are separate from the cranium in the embryo, but are firmly united to it in the adult. A thin median cartilage, the *inter-nasal septum*, separates the two olfactory capsules from each other. The cranial roof in this region is incomplete, there being a large *anterior fontanelle* covered over only by a sheet of connective tissue. On either side of this fontanelle lie two small apertures for the dorsal exit of the *ophthalmicus profundus nerve*. Within each olfactory capsule there is a large opening leading into the cranial cavity, through which the *olfactory nerve* enters the olfactory sac of its own side. In front of the anterior fontanelle arise a pair of *dorso-lateral cartilages*; these cartilages run forward to converge and meet in front with a *median ventral cartilage*, the three cartilages together forming the skeleton of the snout or *rostrum*.

The *visceral skeleton* is composed of a paired series of seven cartilaginous half-hoops encircling the buccal cavity and the pharynx. The first pair of these hoops or arches gives rise to the jaws, the second to the suspensorium, and the last five support the gills.

The first or *mandibular arch* (fig. 49) is highly specialized; each half divides into two segments: an upper *palato-pterygo-quadrato* and a lower *Meckel's cartilage*. The two palato-pterygo-quadrates support the anterior margin of the mouth and unite with each other in front to form the *upper jaw*, while the two Meckel's cartilages extend

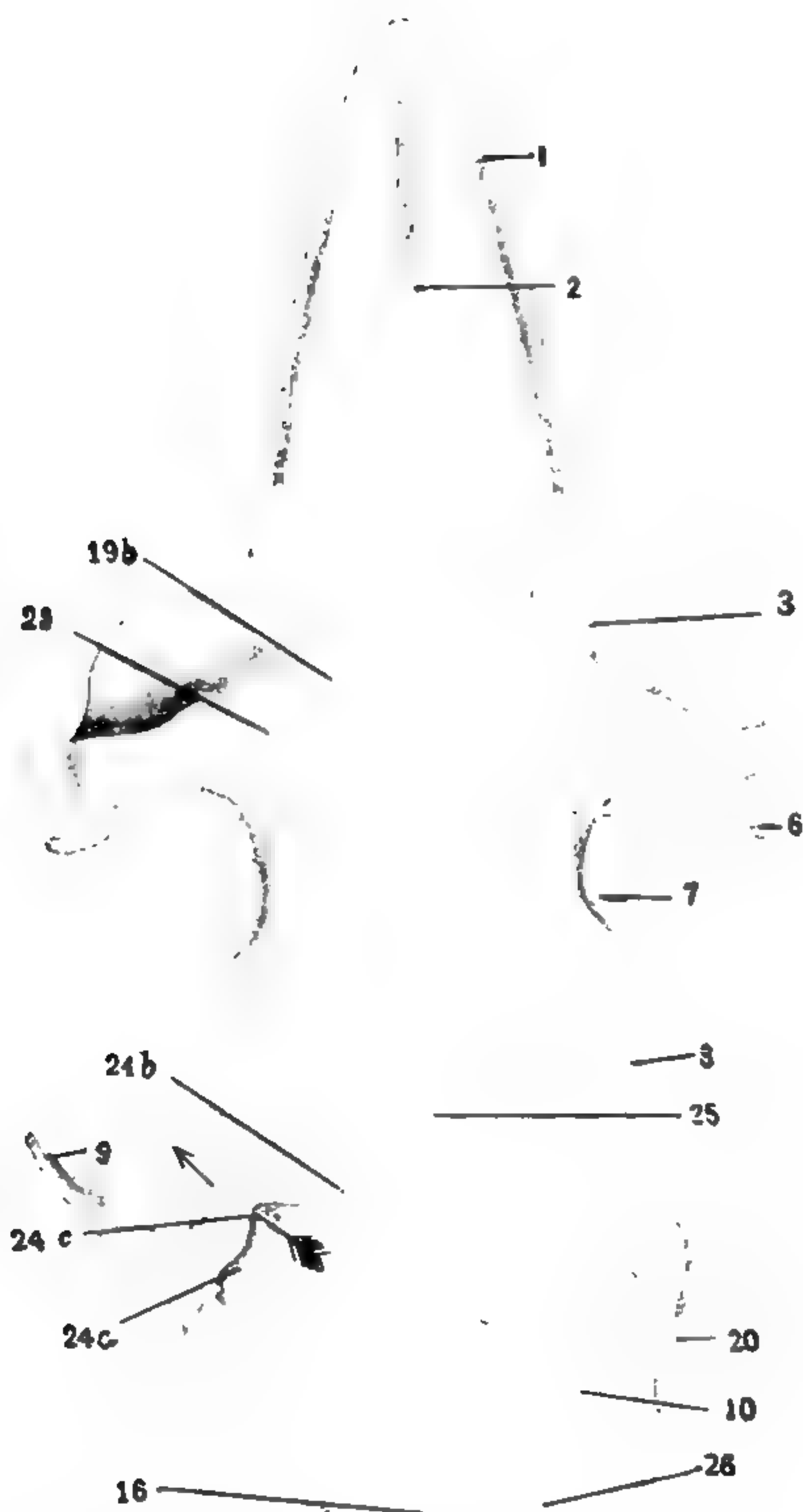


Fig. 48—Ventral view of the skull. 1, dorso-lateral cartilage of rostrum; 2, ventro-median cartilage; 3, olfactory capsule; 6, pre-orbital process; 7, accessory cartilage of the infra-orbital ridge; 8, floor of the orbit; 9, post-orbital process; 10, auditory region; 16, foramen magnum; 19b, anterior opening of the orbito-nasal canal; 20, articular surface for the hyomandibula; 23, ethmo-palatine ridge; 24a, carotid canal; 24b, opening for the entrance of the internal carotid artery into the cranium; 24c, opening for the entrance of the stapedial artery into the orbit; 25, floor of cranium; 26, foramen for the exit of the tenth nerve (\times cir 2).

along the posterior margin of the mouth and unite to form the *lower jaw*. Each palato-pterygo-quadrate is a stout curved rod which is compressed posteriorly and bears a deep groove along the anterior two-thirds of its ventral border. Just behind its anterior end, it gives off an *orbital process* to which is attached the *ethmo-palatine ligament* connecting the upper jaw with the cranium. The anterior ends of the two palato-pterygo-quadrate are also joined together by ligaments, while their posterior ends fit on the articular surfaces of the two Meckel's cartilages. Several rows of teeth are imbedded in the mucous membrane lining the deep grooves of the upper jaw. Each Meckel's cartilage is laterally compressed, broad behind but narrow in front; it lies parallel to the palato-pterygo-quadrate and bears teeth in shallow grooves along its dorsal border. At its posterior end each cartilage bears an articular surface for the upper jaw and also gives attachment to short ligaments that run obliquely from this region to the palato-pterygo-quadrate, thus connecting the upper and lower jaws.

The second or *hyoid arch* consists of three segments: a dorsal *hyomandibula* (fig. 49), a lateral *cerato-hyal* and a ventral *basi-hyal* (fig. 50). The *hyomandibula* is a short stout rod suspended obliquely downward from the side of the cranium, where it fits into a triangular depression just below the post-orbital groove; its distal end articulates with the palato-pterygo-quadrate, the Meckel's cartilage and the cerato-hyal. Thus the upper and lower jaws are not directly articulated with the cranium but are only connected with it through the hyomandibular cartilage. The hyomandibula¹ thus serves to suspend the jaws from the cranium: such a *suspensorium* is called *hyostylic*.

In the Notidani (P. 5, *Hexanchus* and *Heptranchias*) the upper jaw has a double suspension: it articulates directly with the cranium and is also suspended by the hyomandibula; such a double suspension is termed *amphistylic*. But when the upper jaw becomes definitely fused with the cranium, the suspensorium is termed *autostylic*. This type of suspensorium takes two forms: in the Holocephali the upper jaw is fused with the cranium but the hyoid arch remains complete and free from the cranium; this form of suspension is called *holostylic*; in the Dipnoi and all Tetrapods, however, the hyoid arch becomes broken up and its hyomandibula also fuses with the cranium to serve in the auditory region: such a condition is termed *autostylic* or *craniostylic*.

The *cerato-hyal* is slightly longer than the hyomandibula and lies in the floor of the buccal cavity behind the Meckel's cartilage, articulating with the median basi-hyal at its lower end. The hyo-

¹The hyomandibula is further secured to the skull by means of a strong ligament that passes from the sub-orbital ridge to the hyomandibula. Several other ligaments connect the hyomandibula with the palato-pterygo-quadrate.

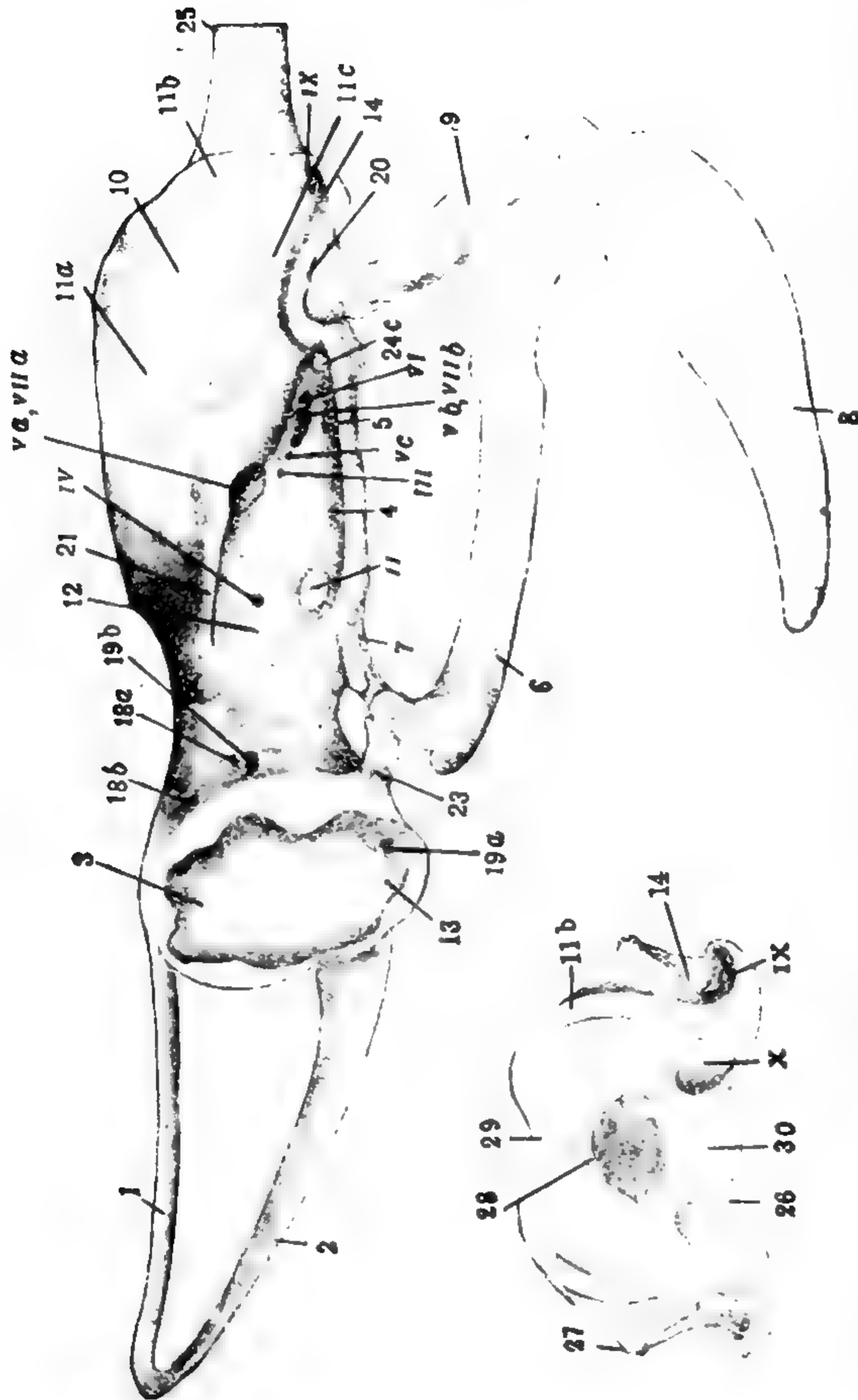


Fig. 49—Side view of the skull and jaws. 1, dorso-lateral cartilage of rostrum; 2, ventro-medial cartilage; 3, olfactory capsule; 4, foramen for the spiracular epibranchial artery; 5, inter-orbital canal; 6, palato-pterygo-quadrates; 7, antorbital process; 8, Meckel's cartilage; 9, hyomandibula; 10, auditory region; 11a, 11b, and 11c, ridges of the anterior, posterior and horizontal semi-circular canals respectively; 12, orbit; 13, aperture for the anterior facial vein; 14, post-orbital groove; 15a, 15b, anterior and posterior foramina for the ophthalmicus profundus nerve; 16a, 16b, anterior and posterior openings of the orbito-nasal canal; 17, articular surface for the hyomandibula; 18, supra-orbital ridge; 19, foramen for the internal carotid artery; 20, vertebral column; 21, occipital condyle; 22, base of post-orbital process; 23, occipital crest; 24, notochord; 25, III, and IV, foramina for the second, third, and fourth cranial nerves; Va, VII, foramen for the fifth and seventh; Vb, VIIb, foramina for the main branches of the fifth and seventh; VI, IX, and X, foramina for the exit of the sixth, ninth, and tenth cranial nerves.

mandibula and cerato-hyal form the anterior wall of the first gill-cleft and carry branched gill-rays along their posterior borders (fig. 50 B). The *basihyal* is a median unpaired plate formed by a fusion of the right and left moieties; it forms the skeletal support for the floor of the buccal cavity, and bears two articular surfaces on each side, one for the cerato-hyal and the other for the hypo-branchial of the first branchial arch.

The remaining five visceral arches support the walls of the pharynx and the gills, and are known as *branchial arches* (fig. 50 A), which gradually diminish in size antero-posteriorly. Each arch is typically divided transversely into four segments on each side: a dorsal *pharyngo-branchial*, an *epi-branchial* and a *cerato-branchial* supporting the sides, and a *hypo-branchial* supporting the floor of the pharynx; these four pieces of each side are connected together in the mid-ventral line by a median piece, the *basi-branchial*. In *Scoliodon* all these cartilages are not present, as some have fused with the adjoining ones and others have been lost.

The *pharyngo-branchials* are long flattened cartilages lying obliquely in the roof of the pharynx; the first three lie one behind the other, while the fourth and fifth are fused together to form one piece. The *epi- and cerato-branchials* are rod-shaped and are grooved along their outer surfaces for the passage of the branchial arteries. The fifth cerato-branchial is much broader than the others and bears a notch along its posterior border for the Cuvierian sinus. The *hypo-branchials* are the most variable segments in this group (fig. 50 A): the first is very small and connects the cerato-branchial of its own arch with the basi-hyal; in a ventral view it is covered over by the lower end of the cerato-hyal; the second curves towards the mid-ventral line and meets its fellow of the opposite side, while the third and fourth articulate with the anterior border of a median dagger-shaped cartilage, the *basi-branchial*, which represents the fused basi-branchial portions of all the arches. The fifth branchial arch has no hypo-branchial and its cerato-branchial articulates directly with the side of the basi-branchial and helps to strengthen and support the roof of the pericardial cavity.

Only the epi- and cerato-branchial segments of the arches bear gill-rays and support the gills. The gill-rays of the hyoidean arch are branched (fig. 50 B), but those of the other arches are simple and unbranched. The inter-branchial septum of each gill extends outwards from the visceral arch to the external integument (fig. 62), and is strengthened by curved cartilaginous rods, the *extra-branchial cartilages* (fig. 51), which lie at right angles to the branchial rays. Four of these cartilages lie at the dorsal edges of the posterior walls

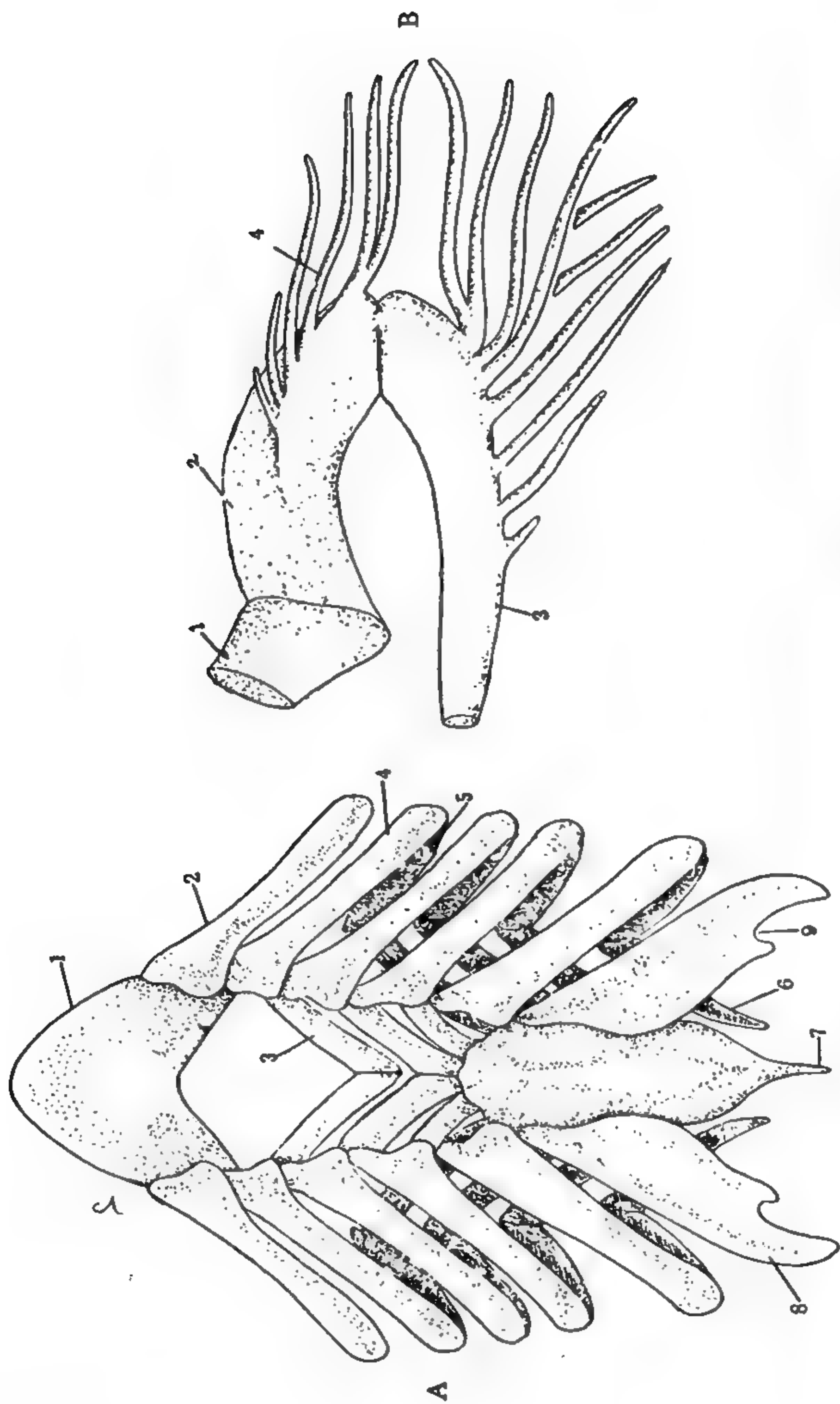


Fig. 50—A Ventral view of the visceral skeleton. 1, basi-hyal; 2, cerato-hyal; 3, second hypo-branchial; 4, first cerato-branchial; 5, first epi-branchial; 6, fused fourth and fifth pharyngo-branchials; 7, basi-branchial; 8, fifth cerato-branchial; 9, notch for the Cuvierian sinus. B. Skeleton of the hyoid arch (ventral view). 1, proximal end of basihyal; 2, cerato-hyal; 3, hymandibula; 4, branched gill-rays.

of the first four gill-pouches and are called *superior extra-branchial cartilages*, while four lie along the ventral edges of the external gill-slits reaching almost to the mid-ventral line, and are known as *inferior extra-branchial cartilages*. The hyoid and the fifth branchial have no extra-branchials.

The skull subserves the two fundamental functions of support and protection: it forms an internal support for the snout, gills and jaws, and at the same time forms a protective case for the brain and receptor-organs.

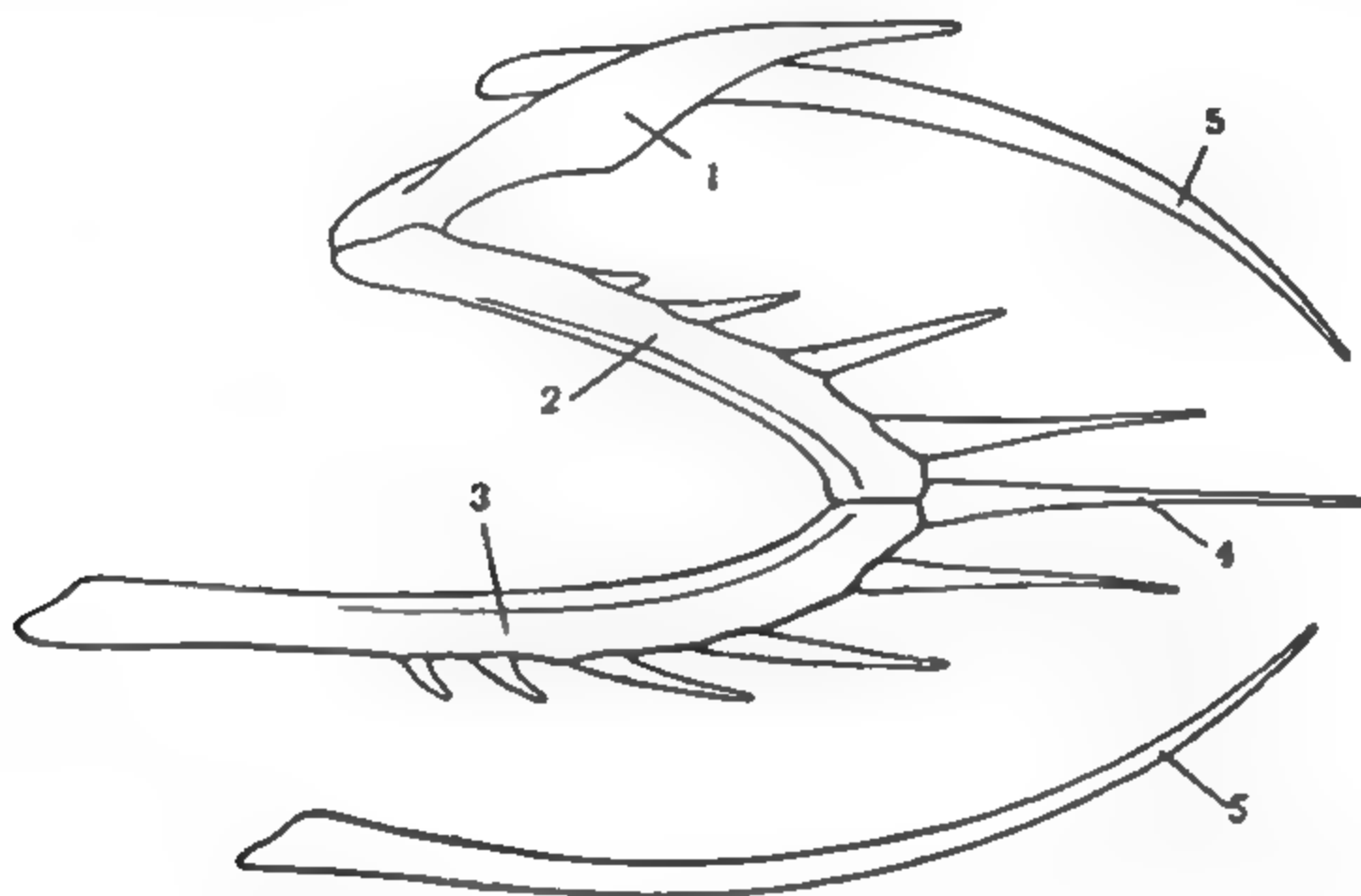


Fig. 51—Part of the skeleton of the first branchial arch. 1. pharyngo-branchial; 2, epi-branchial; 3, cerato-branchial; 4, gill-ray; 5, extra-branchial cartilage.

(b) THE APPENDICULAR SKELETON

The skeleton of the median and paired fins, and the pectoral and pelvic girdles constitute the appendicular skeleton which supports the fins and provides for their articulation with the body.

The skeleton of the *two dorsal* and the *median ventral* fins consists of a series of cartilaginous rods called *somactidia* or *pterygiophores*, which bear distally a double series of numerous horny fin-rays or *ceratotrichia*. Each somactid is divided typically into three segments, the proximal, mesial and distal segments, the segments of the adjoining somactidia tending to fuse at their bases. The *first dorsal fin* is supported by twenty-one somactidia, the proximal segments of which are fused along the posterior border of the fin to form an obliquely horizontal axis in this region (fig. 52). A wide strip of ligamentous tissue connects the somactidia of the fin with the vertebral column. The *second dorsal* and the *median ventral* are built on the same plan as the

first dorsal. In the caudal fin there are no somactidia, but the neural and haemal spines of the vertebral column are elongated and flattened to support the dorsal and ventral lobes of the fin (fig. 46 D).

The *pectoral girdle* lies immediately behind the last branchial arch and consists of two half-hoops of cartilage fused together in the mid-ventral line but free and far apart at their dorsal ends. The girdle is imbedded in the muscles of the trunk and lies vertically within the body-wall with a pectoral fin attached on either side.

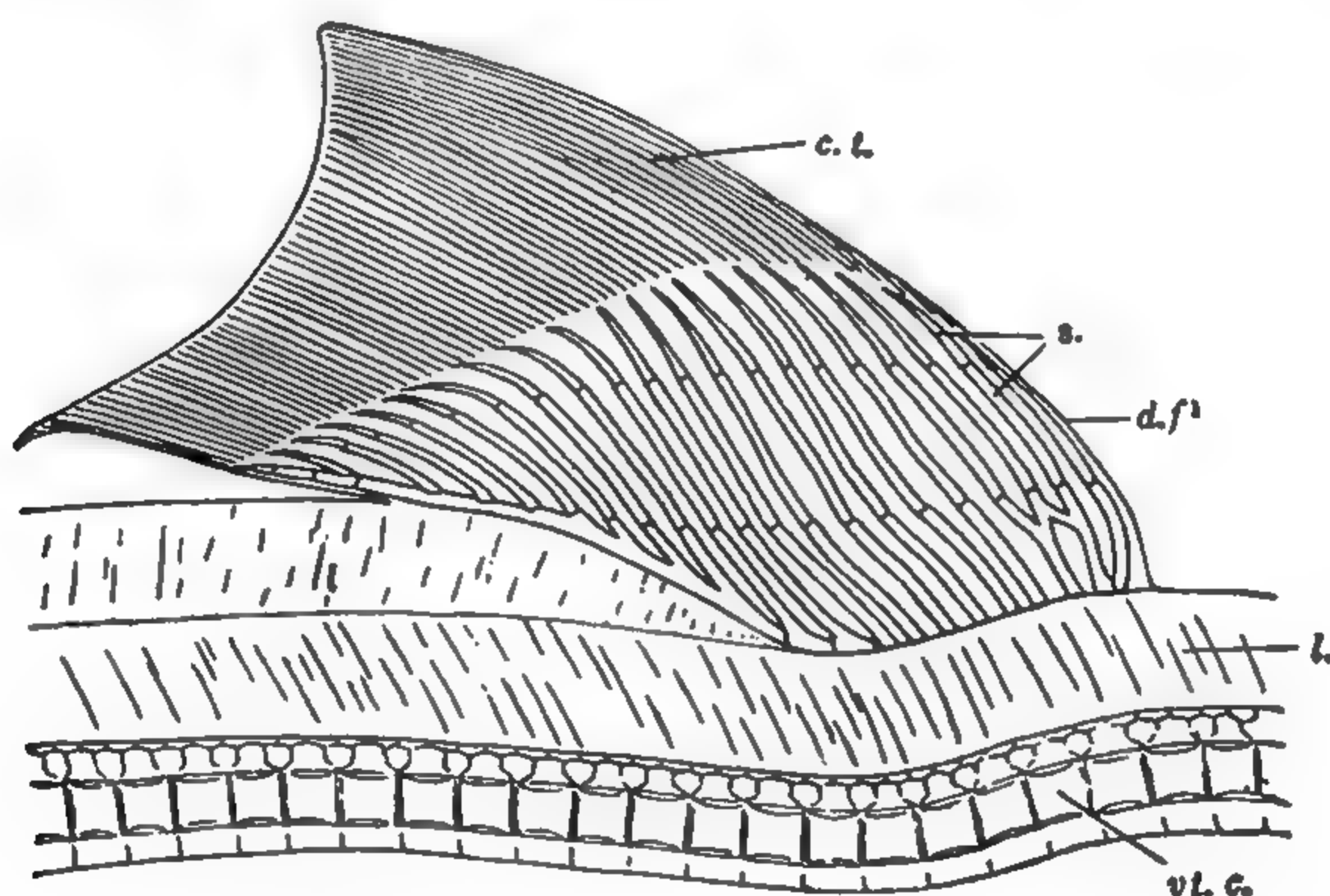


Fig. 52—The vertebral column and the skeleton of the first dorsal fin as seen from the right side. The skeleton of the fin shows the concrescence of the basal segments of the posterior somactidia to form a posterior axis. *c.t.*, ceratotrichia; *d.f¹*, first dorsal fin; *s.*, somactidia; *l.*, ligament; *v.l.c.*, vertebral column. (About natural size).

The ventral portion of each half-hoop, the *caracoid*, is thin and flattened and supports the floor of the pericardial cavity, while the dorsal portion or *scapula* is thick and rod-like. At the junction of the scapular and coracoid portions, along the outer border, there is a triple facet for the articulation of the basal cartilages of the pectoral fin. Just above this facet, there is a large foramen (fig. 53, *for²*.) for the exit of the brachial artery and nerve. This foramen leads into a passage in the girdle, which divides into dorsal and ventral canals, opening on the upper and lower surfaces of the fin by separate foramina (fig. 53, *for¹*).

The skeleton of each pectoral fin consists of three *basal* cartilages, called the *propterygium*, *mesopterygium* and *metapterygium*, and a large number of segmented *radial* cartilages. The propterygium and mesopterygium bear each two segmented radials, while the metapterygium is an elongated cartilage supporting the greater part of the inner border of the fin; it bears about eighteen radials, the distal pieces of which are very long and extend into the body of the fin and support the ceratotrichia. Sometimes the distal end of the metapterygium is formed by a separate small flattened cartilage.

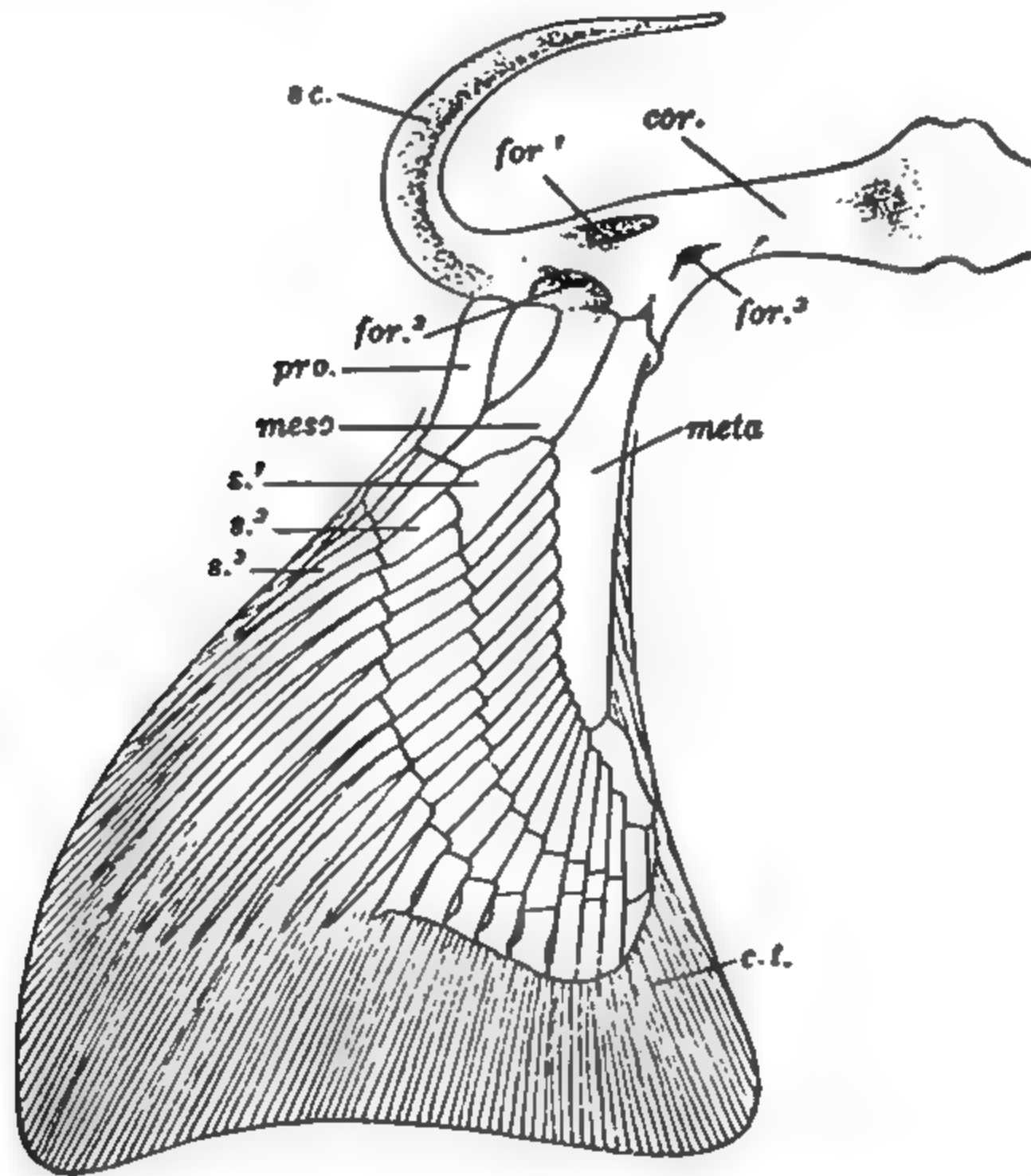


Fig. 53—Ventral view of the left half of the pectoral girdle and fin. *cor.*, coracoid cartilage; *c.t.*, ceratotrichia; *for. 1*, *for. 2*, *for. 3*, foramina for the brachial artery and nerve; *pro.*, propterygium; *meso.*, mesopterygium; *meta.*, metapterygium; *sc.*, scapula; *s. 1*, *s. 2*, *s. 3*, proximal, mesial and distal somactidia. (\times cir. $1\frac{1}{2}$).

The *pelvic girdle* (fig. 54) consists of a flattened rod of cartilage situated transversely in front of the cloaca. At each end of the girdle there is a small foramen for the passage of a nerve. The skeleton of the pelvic fin consists of a curved basal cartilage, the *basipterygium*, which articulates anteriorly with the pelvic girdle, and fifteen or more slender *radials* attached to the outer border of the basipterygium;

at the distal ends of the radials are attached small polygonal cartilages bearing the ceratotrichia.

In the male the tubular cartilage of each clasper (fig. 54) is grooved dorsally, and the edges of the groove are so rolled as to carry the outer skin along with them, thus enclosing the groove in a split tube open at both ends. Distally the groove ends in a sharp *style* enclosed in two flattened plates of cartilage known as *sheathing plates* (fig. 54, *dorsal and ventral plates*). A small *accessory cartilage* with a serrated edge lies at the upper end of the style.

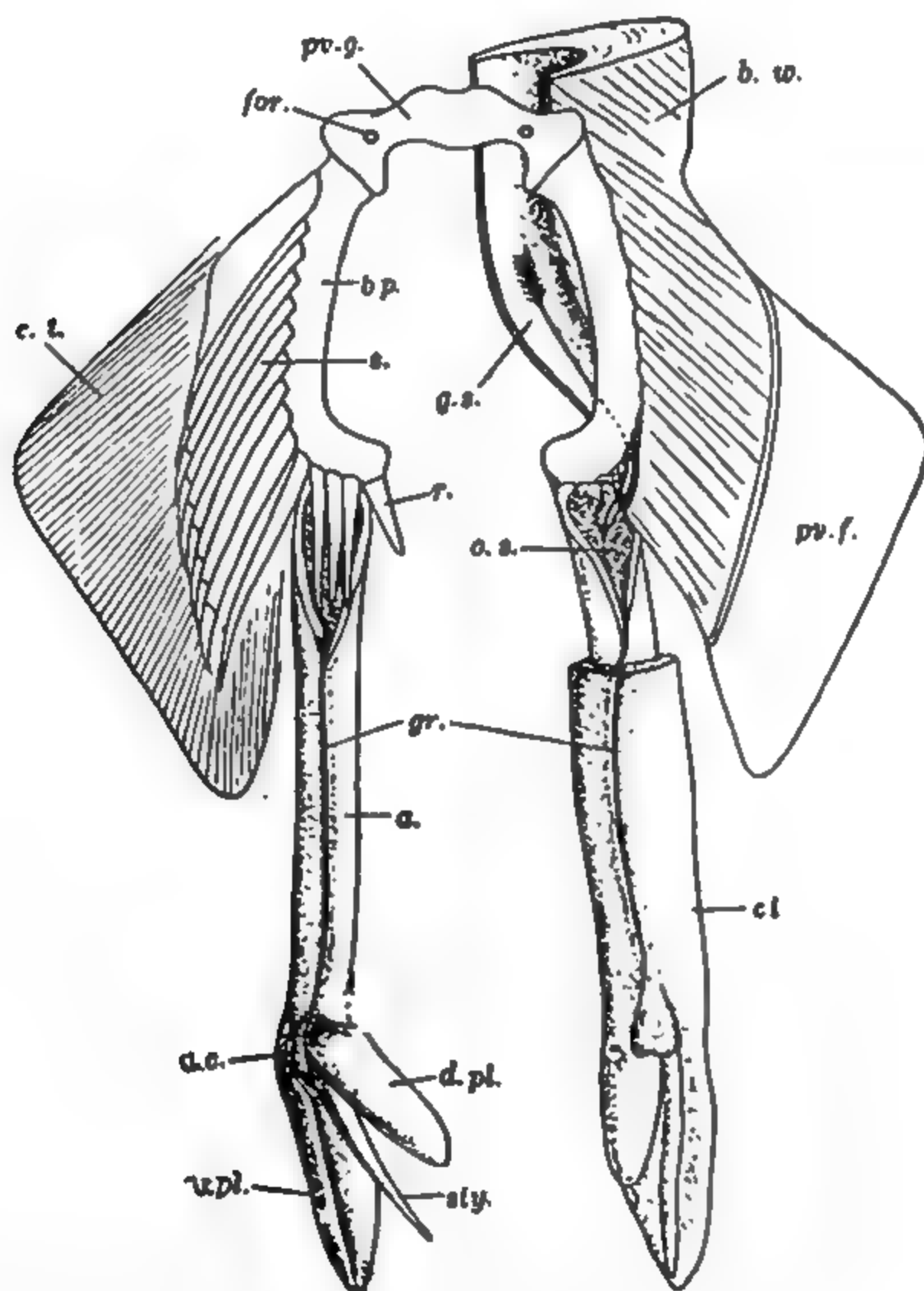


Fig. 54—Dorsal view of the pelvic girdle and fins of a male with the skeleton exposed on the left side. *a.*, axial cartilage of clasper; *a.c.*, accessory cartilage; *b.w.*, portion of the body-wall; *cl.*, clasper; *c.t.*, ceratotrichia; *d. pl.*, dorsal covering plate; *for.*, nerve foramen; *gr.*, groove of clasper; *g.s.*, glandular sac; *o.s.*, opening of glandular sac; *pv.f.*, pelvic fin; *r.*, modified radialis; *pv.g.*, pelvic girdle; *s.*, somactidia; *sty.*, style; *v.pl.*, ventral plate. (\times cir. $2 \frac{1}{3}$).

CHAPTER V

THE MYOTOMES AND LOCOMOTION

The muscles of the shark form the greater part of the bulk of the body and lie closely packed together between the skin and the skeleton. In the region of the trunk and tail the muscles are highly developed and present a perfectly segmental arrangement, consisting of a paired series of muscle-segments or *myotomes* (*myomeres*) separated from one another by partitions of tough connective tissue, the *myocommata*. Each myotome is sharply bent forward and backward four times along its course from its dorsal to its ventral end, and presents a zig-zag appearance (fig. 43 A). Successive myotomes, therefore, present a cone-in-cone arrangement in a surface view, but in a transverse section appear as several bundles of concentrically arranged muscle-lamellae placed one below the other dorso-ventrally (figs. 61 and 84).

The muscle-fibres in each myotome run parallel to the length of the body; when these fibres contract they exert a pull on the myocommata which are inserted internally on the vertebral column and externally on the skin, and thus bring about a flexion both of the backbone and of the rest of the body.

In the trunk the muscular layer is greatly thickened dorsally on each side of the vertebral column (fig. 60) and consequently the body-cavity enclosing the internal organs is pushed towards the ventral side. In the region of the tail, however, the muscles are equally developed all round the vertebral column and occupy the whole of the area between the skin and the vertebral column (fig. 58; 32).

In the region of the head the muscles are highly specialized and do not show any trace of segmentation, being chiefly concerned with the movements of the jaws, eyes and the pharynx. The muscles of the branchial region, arranged around the gill-pouches and gill-arches, also do not exhibit any marked segmentation, nor do the special muscles developed in connection with the median and lateral fins. Thus it is clear that the primitive segmental arrangement of the myotomes is lost in the head and is greatly modified in the region of the gills and the fins.

The locomotion of fishes forms an interesting problem which

has been elucidated only recently by Breder¹ and Gray². It was long believed that the fins of fishes are employed for ordinary slow progress in water, but when danger threatens or the prey is in sight, the fish dashes forward by quick lateral movements of its tail and tail-fin. This explanation has now proved erroneous. By taking a series of photographs, at definite intervals of time, of a swimming fish against a background marked with a graduated scale, Gray has been able to record: (a) the motion of the body of the fish relative to the surrounding water, and (b) the movements of each part of the body relative to the other parts. To a casual observer the forward progression of a shark appears to be due to the transverse strokes executed by its tail across the direction of locomotion of the shark, but photographic records show that the whole of the body takes part in the movement of progression and that *waves of curvature* pass alternately along each side of the entire body, right from the head to the tail. These waves have a more or less constant wavelength but a progressively greater transverse amplitude as they pass from the head to the tail. At the head the amplitude of each wave is small, but it increases steadily as the wave passes backward, and is greatest at the tail end; that is the reason why the eye notices readily the swing of the tail from side to side, but fails to observe the lateral movements of the anterior and middle parts of the body.

These waves of curvature of the body are produced by a succession of longitudinal waves of contraction on alternate sides of the fish. The contraction of the longitudinal muscle-fibres of successive myotomes of one side produces a wave, and as soon as this wave travels backward, a second wave follows on the opposite side and so on. This contraction of successive myotomes resulting in a wave of contraction is called *metachronal contraction*. Fig. 55 gives an idea of the manner in which the body is thrown into waves of curvature as a result of this metachronal contraction of the myotomes, and also shows how the flexure may be traced from the head to the tail.

How do these wave-like flexions of the whole body (head, trunk and tail) propel the fish forward? On a reference to figs. 55 and 56 it will be seen that each portion (or sector) of the body in a swimming fish moves in such a way that its leading surface (*i.e.* the

¹ Breder, C. M.—"The Locomotion of Fishes," Zoologica, 4, 159 (1926).

² Gray, J.—"Studies in Animal Locomotion. I. The Movement of Fish with special reference to the Eel." Journ. Exp. Biol., vol., 10, 88, (1933).

.. —"Studies in Animal Locomotion. II. "The relationship between waves of muscular contraction and the propulsive mechanism of the Eel" vol. 10, 386 (1933).

.. —"Muscular Movements of Fishes". "Nature," 131, 825 (1933).

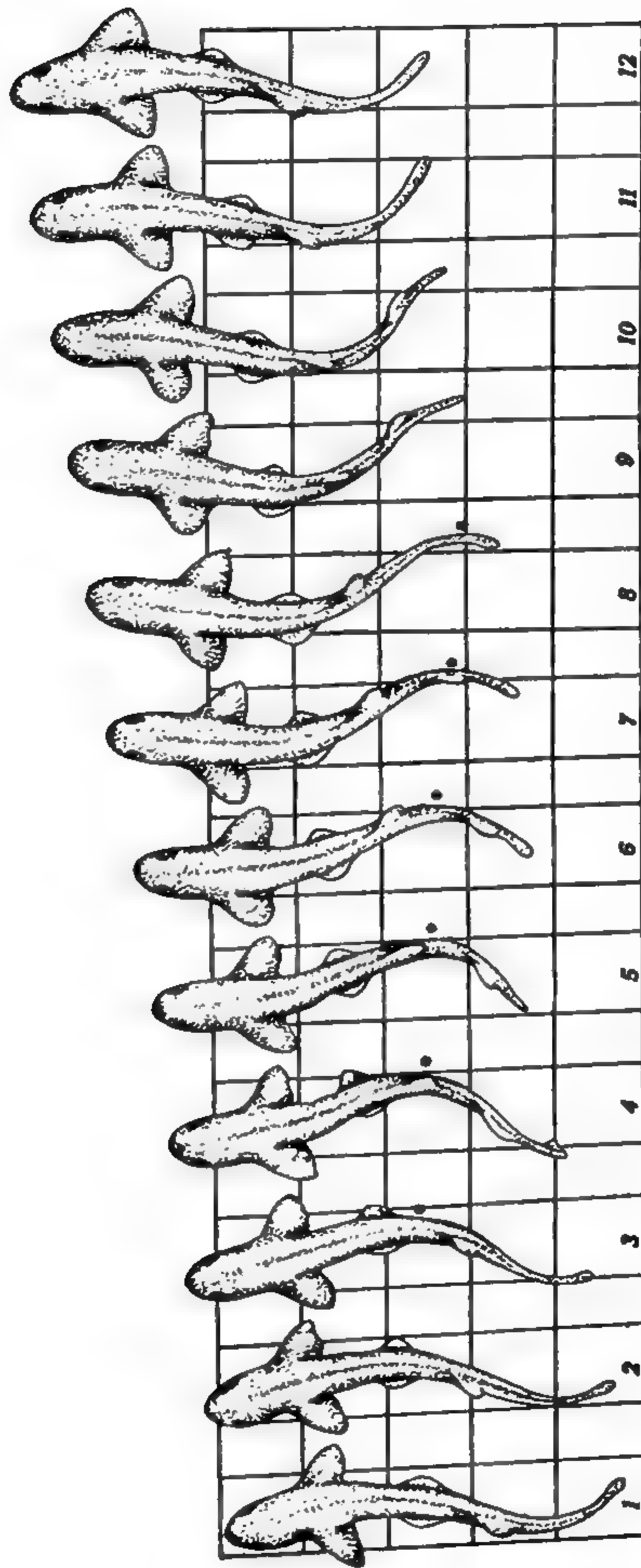


Fig. 55—Successive positions of a dogfish during a period of 1.10 seconds. The photographs were taken at intervals of 0.10 second. The side of each square is 3 inches. Note the large amplitude of the movements of the body and tail. The crest of a wave is marked by a black dot in photographs 3-8. (By kind permission of Professor J. Gray).

surface towards the direction of transverse movement) is inclined at an angle to its own path of motion. In fig. 56 are shown two adjoining sectors of the body, one moving from right to left and the other from left to right during the passage of a complete wave of curvature, the leading surface in both cases being shown by a thick black line. It will be seen that in both sectors this leading surface is always directed obliquely backward relative to the path of motion of the fish as a whole. The pressure of the fish's body against the surrounding water is exerted always by the leading surface. The water is thereby "kicked" obliquely backward on both sides of the axis of forward movement by each sector of the fish's body. The resultant reaction of water to these obliquely backward thrusts given alternately by each side of the body is to give the body of the fish as a whole a forward thrust; and this reaction will continue as long as waves of curvature traverse the body alternately on each side, and exert obliquely backward thrusts on the surrounding water.

The movements executed by each sector of the body of the fish closely resemble the movements of the blade of an oar when sculled from the back of a boat. The underlying mechanism compares closely with that of a typical screw-propeller which consists of a number of inclined plates which by their motion through water generate a force at right angles to their surfaces.

Harris¹ has recently studied experimentally the role of the median and paired fins in locomotion and has come to the conclu-

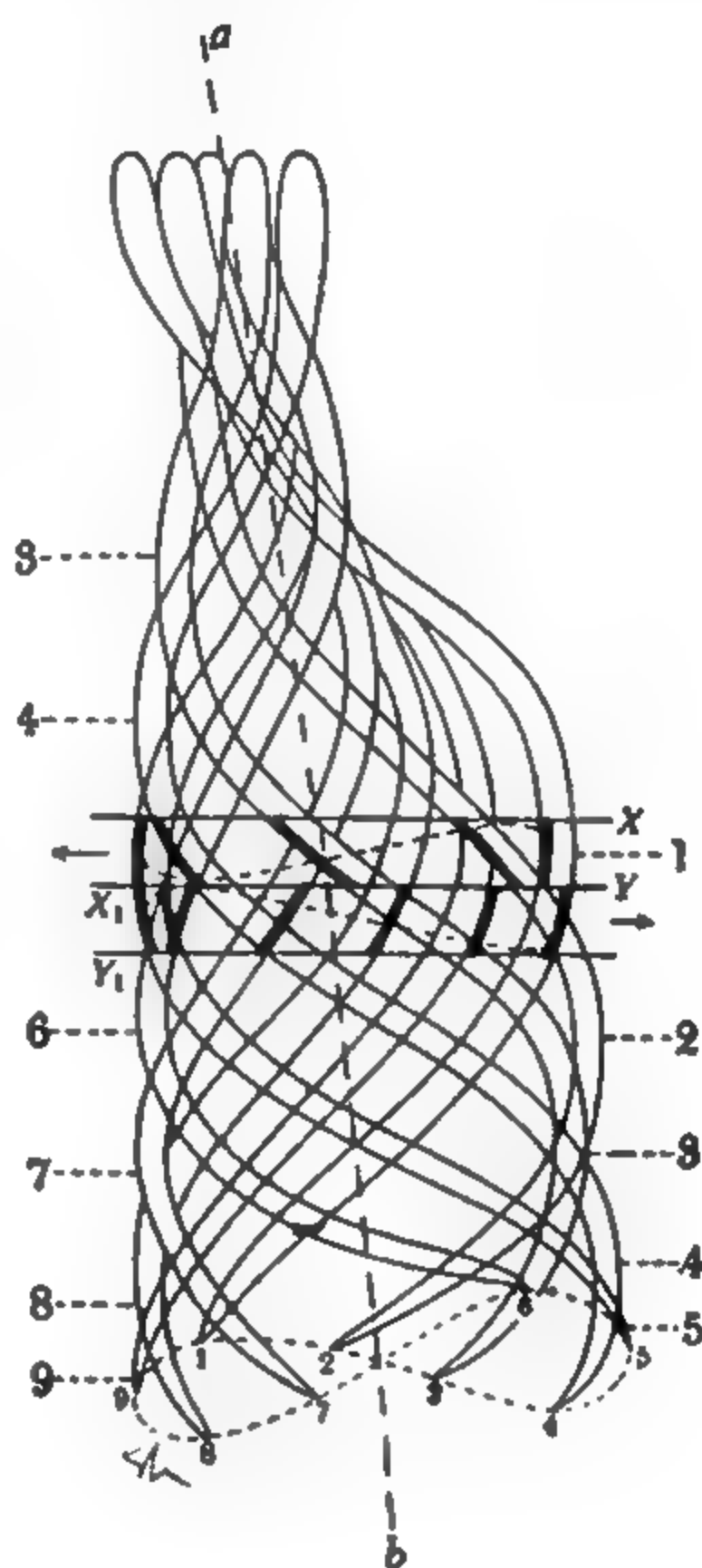


Fig. 56—Enlarged drawings of a young eel (*Anguilla*) arranged to show the movements of short segments of the body during the passage of a complete wave past the segments. The segment $X Y$ is travelling from right to left and is directed obliquely backward to the left. The segment $X_1 Y_1$ is travelling from left to right and is directed obliquely backward to the right. Note that the tip of the tail is moving in a figure of 8 curve. (By kind permission of Professor J. Gray)

¹ Harris, J. E.—"The Role of the Fins in the Equilibrium of the Swimming Fish." I and II, Journ. Exp. Biol. vols., 13 and 15, 1936 and 1938.

sion that the main function of the median and paired fins is to maintain the equilibrium of the body in a swimming fish. Just as a boat in a rough sea is subject to (a) a *rolling* or *yawing* motion, *i.e.*, turning movements in a horizontal plane, and (b) a *pitching* motion, *i.e.*, rising and diving movements in a vertical plane; similarly, a swimming fish has to maintain its equilibrium against these two disturbing factors in water.

The median dorsal fins of a dogfish act as stabilising keels to prevent rolling, and thus help to maintain its equilibrium in the horizontal plane. The paired fins and the caudal fin of the fish, however, are largely concerned with the production of vertical forces and thus affect mainly the pitching equilibrium. The strong lateral movements of the heterocercal tail and tail-fin during swimming, besides giving a forward thrust to the fish, produce a negative pitching reaction making the fish dive head downward; this negative reaction is counterbalanced by a positive pitching reaction (lift force) produced by the paired fins. These paired fins, in fact, are essentially 'elevating planes' in the dogfish. In other words, while the movements of the tail and tail-fin tend to force the nose of the fish downward, the "trailing" movements of the pectoral and pelvic fins tend to force the nose upward with nearly the same amount of force. The heterocercal tail and the paired fins, therefore, neutralize each other's opposed pitching effects, and thus lead to the normal equilibrium of a swimming dogfish. Of the pectoral and pelvic fins, it is the pectorals that largely determine the pitching stability, the contribution of the pelvics being very small.

CHAPTER VI

THE COELOM AND THE ALIMENTARY CANAL WITH ITS ASSOCIATED GLANDS

THE COELOM

The coelom is spacious and is divided into two unequal cavities, the *pericardial* and the *abdominal*, separated from each other by a membranous partition, the *septum transversum*. The small triangular pericardial cavity lies beneath the pharynx and surrounds the heart (fig. 58); it is enclosed between a tightly fitting smooth layer of peritoneum lining the outer wall of the cavity and the inner pericardial layer which adheres closely to the heart itself. The cavity contains a clear colourless fluid, the *pericardial fluid*. The roof of the cavity is supported by the basi-branchial cartilage and the floor by the united coracoids of the pectoral girdle. It communicates with the abdominal cavity through a passage in the septum transversum called the *pericardio-peritoneal canal*.

The *abdominal cavity* is extensive: it surrounds the viscera and communicates with the exterior through a pair of abdominal pores situated on papillae, one on either side of the cloacal aperture. The abdominal cavity is also filled with a colourless coelomic fluid and is lined by the *peritoneum*, which is closely adherent to the inner surface of the muscles of the body-wall, but is free in the mid-dorsal line where it is reflected beneath the vertebral column to form a double fold of membrane, the *mesentery*, by which the gut is suspended in the coelom. The mesentery is incomplete, only the anterior and posterior portions being well developed; the anterior portion forms a large flap, the *mesogaster*, which suspends the stomach, while the posterior portion, the *mesorectum*, suspends the hinder part of the alimentary canal. There are other membranes which attach different organs to one another and are termed the *omenta*. The *gastro-hepatic omentum* connects the liver with the stomach, while the *gastro-splenic omentum* connects the spleen with the stomach.

THE ALIMENTARY CANAL

The alimentary canal comprises the mouth, buccal cavity, pharynx, oesophagus, stomach, intestine and rectum.

The *mouth* is a ventral crescentic opening bounded in front and behind by folds of the integument which are sometimes called the *upper* and *lower lips*. It leads into a spacious dorso-ventrally compressed *buccal cavity*, the roof of which is supported by the base of the cranium and the floor by the flat basi-hyal cartilage. The buccal cavity is lined with a thick mucous membrane raised ventrally into a thick fold to form the so-called "tongue" which is non-muscular and non-glandular. The mucous membrane is rough owing to the presence of dermal denticles, which in the region of the jaws are modified into teeth. The teeth (fig. 43 B) are oblique and have sharp, and more or less compressed, cusps, the edges of which are smooth and non-serrated. They are borne in several parallel rows (fig. 57) on the inner margins of the upper and lower jaws, and are not attached to the cartilages of the jaws, but are merely imbedded in the mucous membrane which is connected with the jaws only by fibrous connective tissue. The teeth are similar in shape and therefore the dentition is described as *homodont*; they are used to catch the prey and prevent its escape but not to crush or masticate it. Of the several rows only one is functional at a time, but when the old teeth get worn out or lost, new teeth migrate upwards over the jaws to take the place of the old: thus *Scoliodon* has a *lyodont* dentition, i.e., it has several sets of teeth functioning in succession. There are no glands in the buccal cavity comparable to the salivary glands of the higher vertebrates.

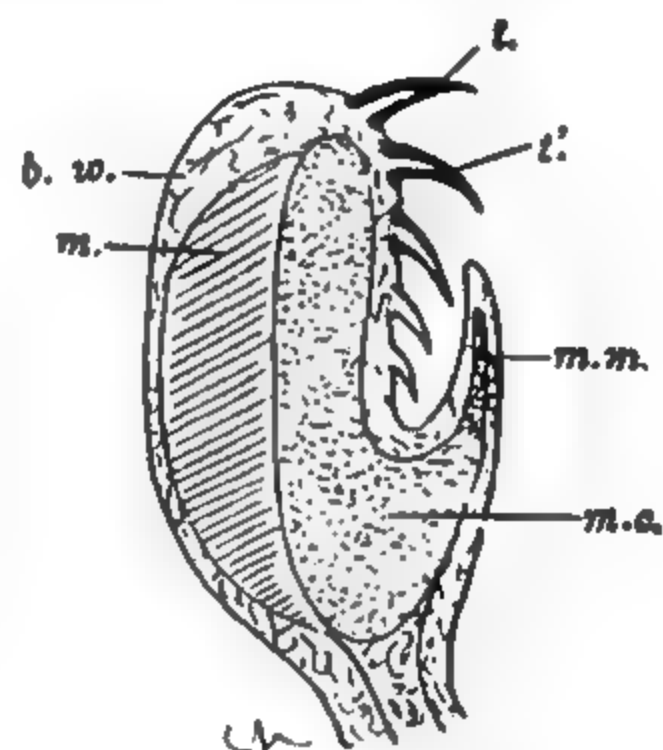


Fig. 57—A transverse section through the lower jaw of *Scoliodon*, showing replacement of teeth. *b.w.*, outer integument; *m.*, muscle; *m.c.*, Meckel's cartilage; *m.m.*, mucous membrane; *t.*, functional tooth; *t\'*, its immediate successor. (\times cir. 4).

The buccal cavity passes insensibly into the *pharynx*, on either side of which lie the internal openings of the spiracle and the five gill-pouches (fig. 59). The vestigial *spiracle* is merely an inconspicuous oval pit with no gill-lamellae or external aperture, but the succeeding gill-pouches are large, although they go on diminishing in size antero-posteriorly. The cavity of the pharynx is lined with mucous membrane containing a large number of dermal denticles which are specially numerous in the regions of the gill-slits.

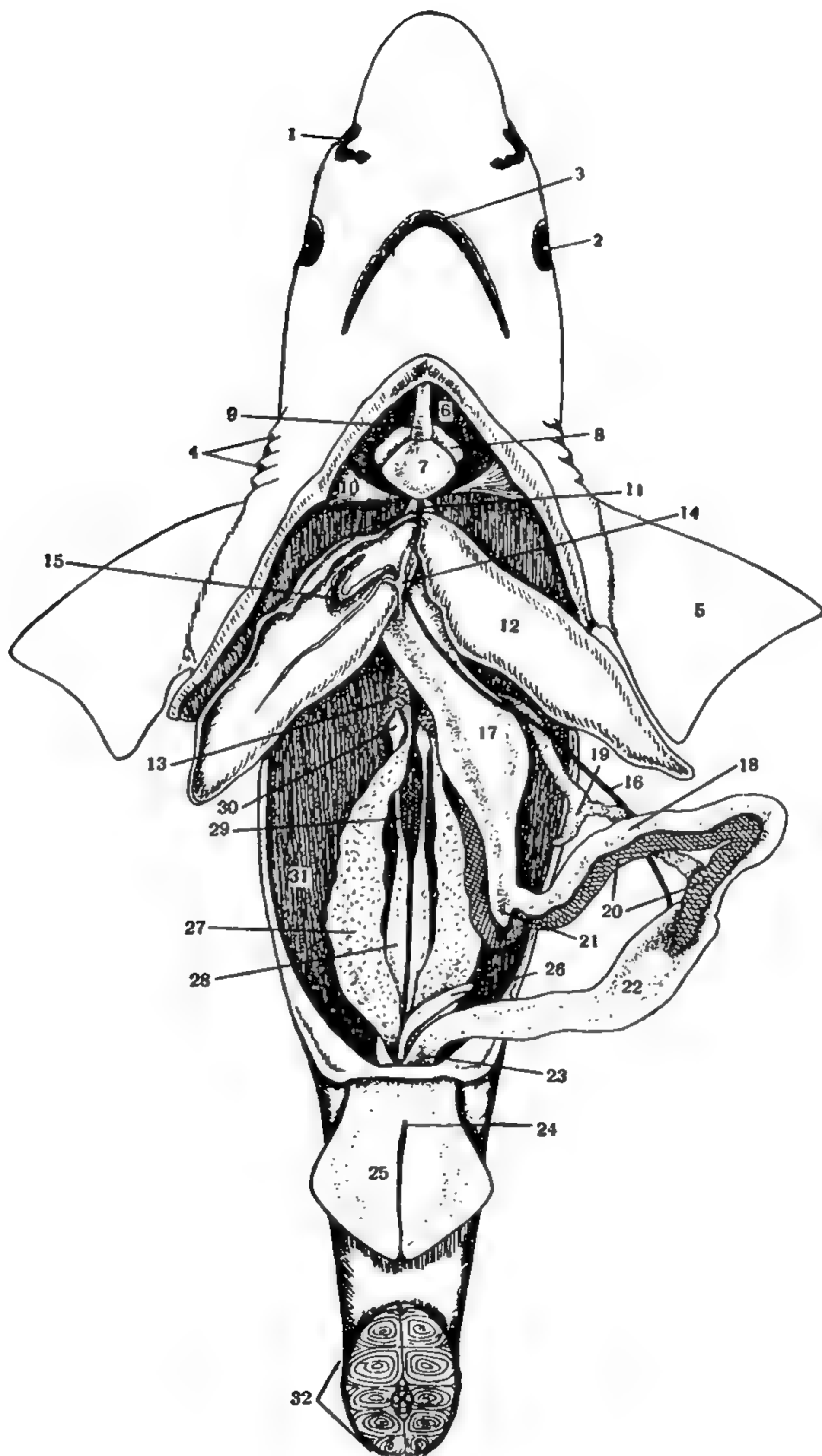
Since the pharynx bears gills, it subserves a digestive as well as a respiratory function. In the development of gill-pouches, five pairs of pharyngeal evaginations

meet similar inpushings of the ectoderm, the ectodermal inpushings carrying dermal denticles with them into the gill-pouches.

The pharynx narrows posteriorly to form the short *oesophagus* which has thick muscular walls with an internal lining of mucous membrane raised into longitudinal folds. The oesophagus widens behind to form the large muscular *stomach*, at the entrance of which the mucous membrane forms a crescentic fold, which acts as a valve and marks the boundary between these two regions of the gut. The stomach is bent on itself and forms a J-shaped organ, the long proximal limb of which extends almost to the posterior end of the abdominal cavity and is called the *cardiac stomach*, while the short distal limb is called the *pyloric stomach*. At the junction of the cardiac and pyloric limbs there is a small outgrowth, the so-called "blind sac". The mucous lining of the cardiac stomach, like that of the oesophagus, is also thrown into prominent longitudinal folds, which are continuous anteriorly with those of the oesophagus but end posteriorly in the depression of the "blind-sac." Some of these folds, however, abut against a circular fold which forms a valve between the cardiac and pyloric limbs. The lining of the pylorus is smooth proximally but is slightly folded distally. At the end of the pylorus there is a circular band of muscle-fibres, called the *pyloric valve*, guarding the entrance into a small thick-walled muscular chamber, the *bursa entiana*, which is followed by the intestine (fig. 59).

The *intestine* is a wide tube, about the diameter of the cardiac stomach in the middle of its length; it runs straight backward in the abdominal cavity and narrows posteriorly to form the *rectum* which opens behind into the *cloaca*. The internal surface of the intestine is increased by a characteristic fold of the mucous membrane, called the *scroll valve*, having one edge attached to the inner wall of the intestine and the other rolled up longitudinally on itself into a scroll, making an anti-clockwise spiral of about two and a half turns (figs. 59 and 61). In a transverse section (fig. 61) the scroll-valve looks like a watch-spring. Externally the line of attachment of the scroll-valve to the wall of the intestine is marked by the anterior intestinal artery and vein. This valve serves not only to increase the extent of the absorptive surface of the intestine

Fig. 58—A ventral view of the internal viscera in a female *Scoliodon sorrakowah*. 1, right naris; 2, eye; 3, mouth; 4, gill-clefts; 5, pectoral fin; 6, pericardial cavity; 7, ventricle; 8, atrium; 9, conus arteriosus; 10, septum transversum; 11, coelomic opening of oviducts; 12, liver; 13, ovary; 14, hepatic portal vein; 15, gall-bladder; 16, bile-duct; 17, cardiac stomach; 18, pyloric stomach; 19, pancreas; 20, spleen; 21, "blind sac"; 22, valvular intestine; 23, rectum; 24, cloacal opening; 25, pelvic fin; 26, rectal gland; 27, epigonal organ; 28, uterus; 29, oviduct; 30, shell-gland; 31, body-wall; 32, section of the tail. (about three-fourths natural size).



but also to retard too rapid a passage of the food through the intestine.

During development the scroll-valve first appears as an elongated ridge running along the inner surface of the intestinal wall: this ridge grows into the lumen of the gut as a sheet of tissue which on reaching the opposite side of the gut-cavity is rolled up into a scroll. In the shark it persists in this condition in the adult, but in many other Elasmobranchs a further twisting takes place which throws the scroll into a spiral, forming a *spiral valve*, as found in *Scyliorhinus*.

The last part of the intestine is the *rectum* into which the tubular *rectal (caecal) gland* opens dorsally. The rectum leads into the *cloaca* into which the alimentary canal as well as the urinogenital ducts open.

THE GLANDS OF THE ALIMENTARY CANAL

The *liver* (fig. 58) is an elongated yellowish gland, consisting of two lobes which extend back along the greater part of the abdominal cavity. These lobes are united anteriorly where they are attached to the wall of the abdominal cavity by a median suspensory ligament. Imbedded in the anterior portion of the right lobe of the liver is a V-shaped thin-walled sac, the *gall-bladder*, which stores the bile secreted by the liver. The gall-bladder is drained by the *bile-duct* or *ductus choledochus* which is joined by several smaller ducts from the right and left lobes of the liver: the duct runs backward parallel to the hepatic portal vein, along the ventral margin of the mesentery, and opens into the intestine just near the commencement of the scroll-valve. In a full grown specimen the bile-duct is about 3 cm. long (fig. 58).

The *pancreas* is a compact bilobed gland situated in the angle between the two limbs of the stomach. It consists of: (a) *dorsal lobe* running parallel to the posterior part of the cardiac stomach, and (b) a *ventral lobe* lying closely applied to the pyloric stomach. The pancreatic duct traverses the whole length of the gland and opens into the intestine just opposite the aperture of the bile-duct (fig. 59).

The *caecal (rectal) gland*¹ is a small diverticulum from the dorsal wall of the rectum. Its significance is incompletely understood but it is present in all living Elasmobranchs. There is no doubt that it discharges a fluid into the intestinal lumen but the physiological effect of the fluid is unknown. The highly vascular nature of the organ, the intimate relation of the glandular tubule-cells with the blood-stream, and the presence of simple lymphoid tissue point to an obscure blood-function.

¹ Crofts, D.R.—“The Comparative Morphology of the Caecal Gland (Rectal Gland) of Selachian Fishes” Proc. Zool. Soc., 1925.

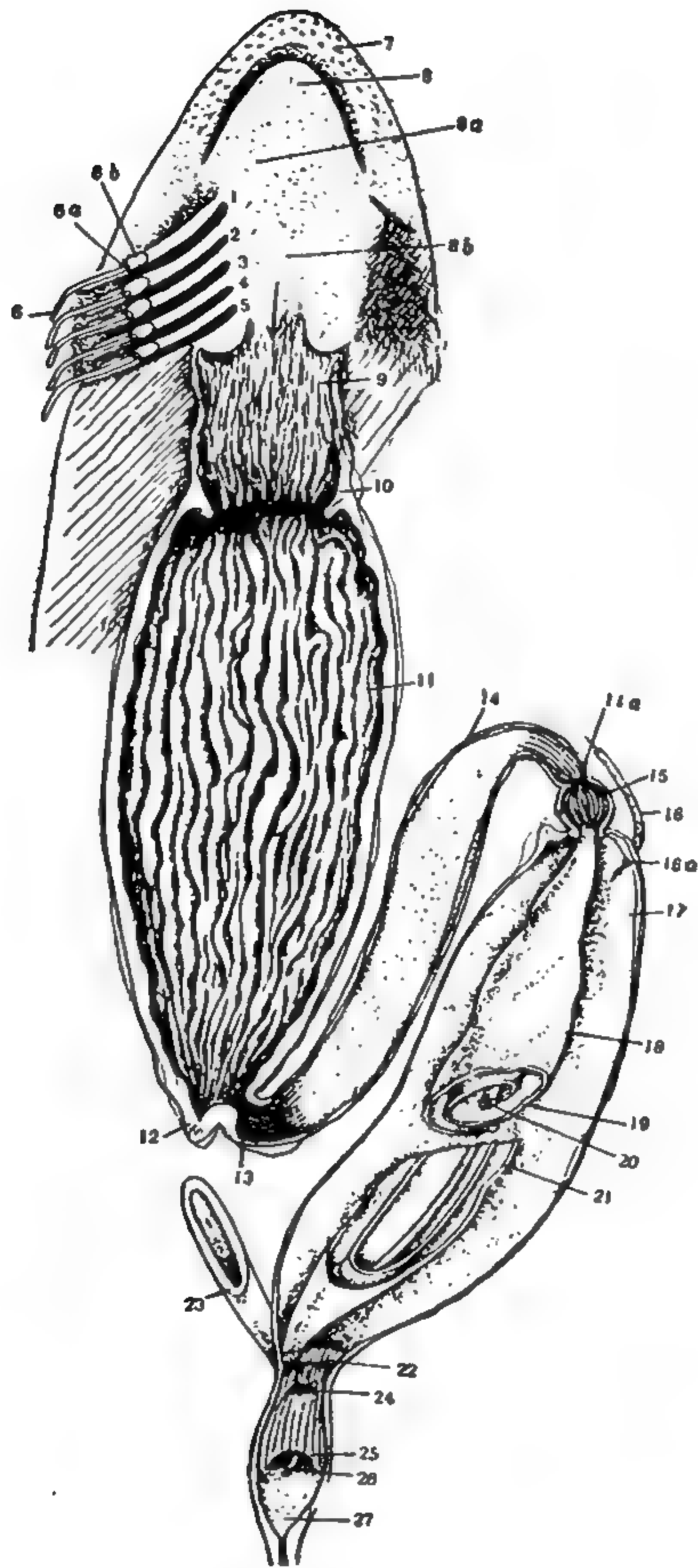


Fig. 59—A dissection of the alimentary canal. 1,2,3,4,5, five gill-pouches; 6, inter-branchial septum; 6a, afferent branchial artery; 6b, cartilage of the branchial arch; 7, lower jaw with teeth; 8, tongue; 8a, buccal floor; 8b, pharynx; 9, mucous lining of the oesophagus; 10, valve at the entrance to the stomach; 11, mucous membrane of cardiac stomach; 12, blind sac; 13, sphincter valve at the entrance of the pyloric stomach; 14 pyloric stomach; 14 a, pyloric valve; 15, bursa entiana; 16, bile-duct; 16a, opening of the bile-duct; 17, intestinal wall; 18, mucous membrane of the scroll valve; 19, the scroll valve in transverse section; 20, intra-intestinal artery; 21, the scroll valve in longitudinal section; 22, valve at the entrance to the rectum; 23, caecal (rectal) gland; 24, opening of caecal gland; 25, opening of the uteri into the cloaca; 26, urinary papilla; 27, cloaca. (semi-diagrammatic).

PHYSIOLOGY OF DIGESTION¹

Sharks feed mainly on other fishes, but the diet may also include rock-crabs, lobsters and spider-crabs. As a rule, dog-fishes and sharks swallow their food entire without mastication. Since there are no salivary glands in the mouth, there is no digestion in the buccal cavity, the buccal mucus containing only mucin to lubricate the food but no digestive ferment. The oesophagus also has

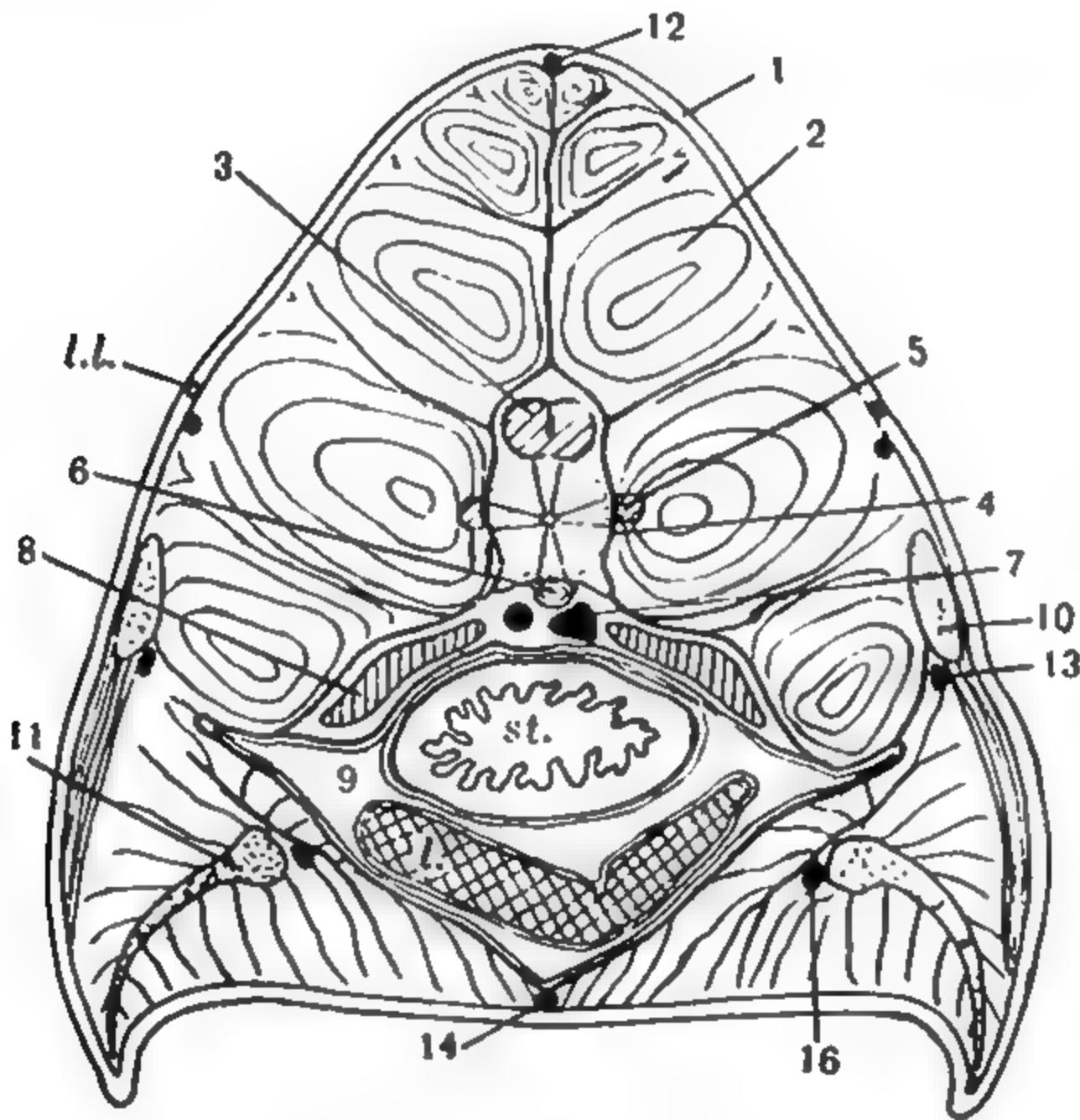


Fig. 60—A transverse section of the body of the shark passing through the stomach and liver. 1, integument; 2, myotome; 3, spinal cord; 4, vertebra; 5, spinal nerve; 6, dorsal aorta; 7, right posterior cardinal vein; 8, kidney; 9, coelom; 10, fifth branchial arch; 11, cartilage of the pectoral fin; 12, dorsal cutaneous vein; 13, inferior lateral cutaneous vein; 14, ventral cutaneous vein; 16, brachial vein: *l.*, liver: *ll.*, lateral line canal; *st.*, stomach (\times cir. 2).

no digestive function. The mucous membrane of the stomach secretes the gastric juice which contains pepsin and hydrochloric acid and converts proteins into syntonin, proteoses and peptones, but can not digest chitin. The pyloric stomach and the scroll-valve have no digestive activity of their own but they activate the pancreas. The pancreas, as a rule, secretes trypsinogen but may secrete trypsin;

¹ This account is based on Michael X. Sullivan's paper on the "Physiology of the digestive tract of Elasmobranchs". Bulletin of the Bureau of Fisheries, Washington, Vol. XXVII. 1907.

it also secretes the starch-splitting ferment amylopsin and the fat-splitting ferment lipase. As the semi-digested food enters the intestine, it is acted upon by the bile and the pancreatic juice. The bile makes the food alkaline and thus helps the action of the pancreatic juice. The digested food is absorbed into the blood over the extensive surfaces of the intestine and the scroll-valve.

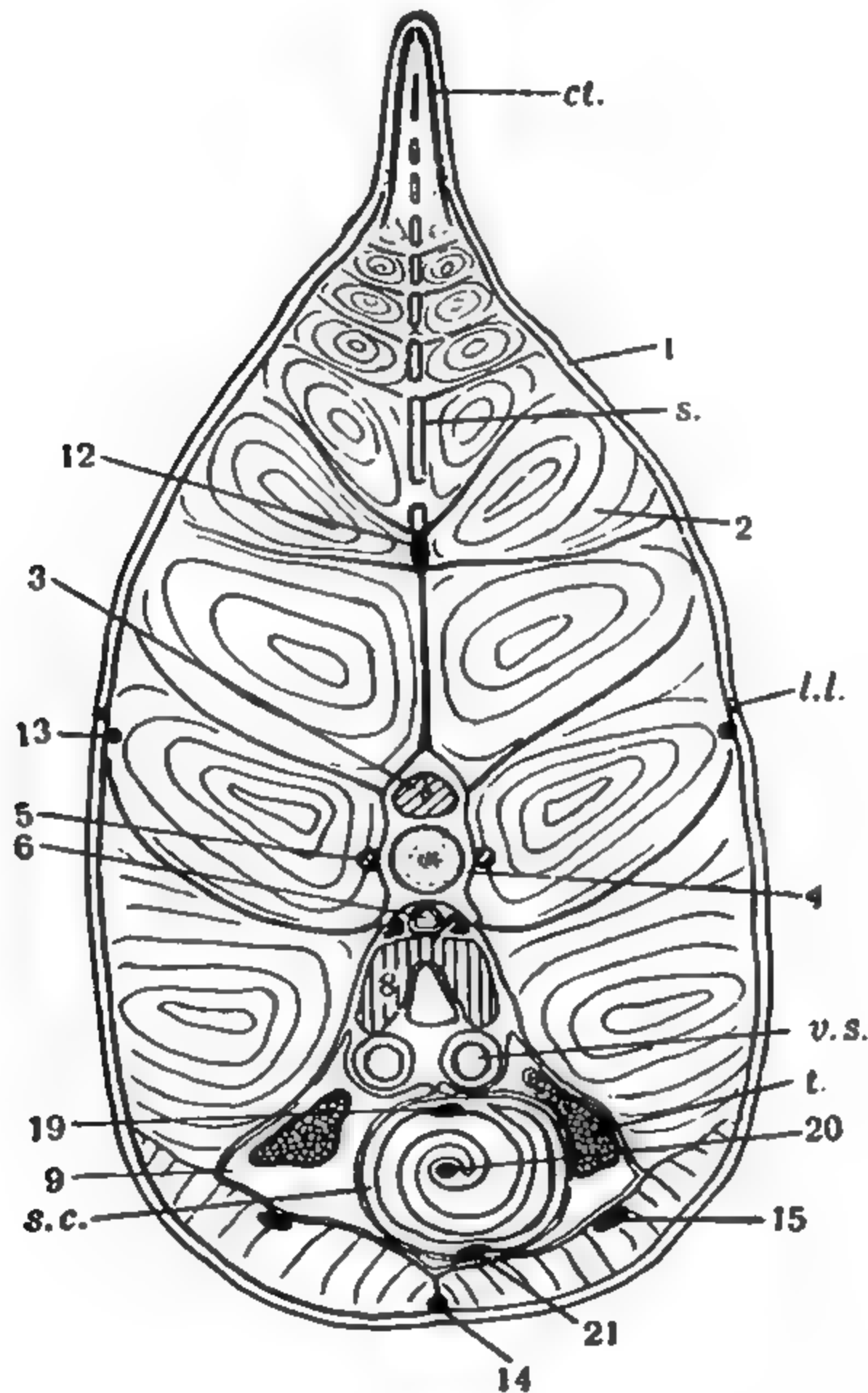


Fig. 61—A transverse section of the body of a male shark passing through the intestine, "scroll valve", and the testes. 1, integument; 2, myotomes; 3, spinal cord; 4, vertebra; 5, spinal nerve; 6, dorsal aorta; 8, kidney; 9, coelom; 12, dorsal cutaneous vein; 13, lateral cutaneous vein; 14, ventral cutaneous vein; 15, lateral cutaneous vein; 19, anterior intestinal vein; 20, intra-intestinal vein; 21, posterior intestinal vein; *ct.*, ceratotrichia; *l.l.*, lateral line canal; *s.*, somactidia of the first dorsal fin; *s.c.*, intestine enclosing the "scroll valve"; *t.*, testis; *vs.*, vesicula seminalis. (\times cir. 2)

DUCTLESS GLANDS.

The *spleen* (fig. 58) is a large gland consisting of two lobes: the proximal lobe extends along the outer curvature of the cardiac stomach, while the thin elongated distal lobe lies parallel to the pyloric stomach and is closely bound to the ventral lobe of the pancreas.

The *thyroid* is an irregular glandular mass surrounded by a capsule of connective tissue; it lies just behind the symphysis of the lower jaw, ventrally to the basi-hyal cartilage.

The *thymus* appears in the embryo as a series of nodules connected into a chain above the gill-pouches, but it degenerates soon and is absent in a full-grown shark.

CHAPTER VII

THE RESPIRATORY SYSTEM

Like most fishes *Scoliodon* is adapted to respiration in water and breathes by means of gills borne in a series of gill-pouches on either side of the pharynx. Water enters the buccal cavity and pharynx through the mouth and passes out through the gill-slits, bathing the gills on its way through the gill-pouches.

There are five pairs of *gill-pouches*; each pouch is compressed antero-posteriorly and communicates, on the one hand, with the cavity of the pharynx through a large *internal branchial aperture*, and on the other, with the exterior through a narrow *external branchial aperture* (fig. 59). The mucous membrane lining the gill-pouches is raised into a series of horizontal folds, the *branchial lamellae*, which are richly supplied with blood-capillaries; each gill-pouch has thus two sets of gill-lamellae, one on its anterior and the other on its posterior wall. Successive gill-pouches are separated from one another by stout fibro-muscular partitions called the *inter-branchial septa*, the inner or pharyngeal border of each of which is supported by a visceral arch with its branchial rays. Each arch, therefore, alternates with a gill-pouch and supports the posterior set of lamellae of one pouch and the anterior set of lamellae of the next pouch behind. These two sets of lamellae attached to a visceral arch and its inter-branchial septum constitute a *complete gill* or *holobranch* (fig. 62), while a single set makes a *demibranch* or a *half-gill*. Of the two demibranchs of an interbranchial septum, the posterior has longer lamellae than the anterior (fig. 62). A gill-pouch thus includes the posterior demibranch of one gill and the anterior demibranch of the succeeding gill.

The form of gill in which the gill-folds are attached along their whole length to the interbranchial septum is known as *lamelliform* and is characteristic of Elasmobranchs in general. In Teleosts the inter-branchial septum is greatly reduced and the gill-folds are free at their distal ends: such a gill is, therefore, called *filiform* or *pectinate*.

The hyoid arch bears gill-lamellae on its posterior border only, and, therefore, supports only a demibranch; the first four branchial arches bear gill-lamellae on both their anterior and posterior surfaces, and therefore each supports a holobranch, while the fifth branchial arch is entirely gill-less.

The *spiracle* is a vestigial gill-pouch in front of the hyoid arch; it differs from the other gill-pouches in that its internal opening is extremely small, while the external opening is completely closed. In *Scoliodon* it bears no gill-lamellae but that it is a true gill-pouch, which has become vestigial, is shown by the fact that in *Scyliorhinus* and many other Elasmobranchs, it bears minute gill-lamellae on its anterior wall and also opens to the exterior by an external aperture just behind the eye.

MECHANISM OF RESPIRATION.

The fish depresses the floor of the buccal cavity by the contraction of its hypobranchial muscles and consequently the buccal cavity is enlarged and its volume-capacity increased. Simultaneously with the lowering of the floor of the buccal cavity, the mouth is opened and water rushes in to fill the enlarged buccal cavity. The cavity of the pharynx is next enlarged by the expansion of the hoop-like gill-arches, while the external gill-slits are still tightly closed. During the expiratory phase the mouth is closed by the action of the adductor muscles, the pharynx contracts and the water enters the branchial pouches and is then forced out through the external gill-slits by the contraction of the constrictor and inter-branchial muscles. Actual exchange of gases takes place as the water passes over the gill-lamellae, Daniel states that the Port Jackson shark *Heterodontus*, when at rest respires *thirty-five* times in a minute,

PHYSIOLOGY OF RESPIRATION.

Fresh sea-water entering the gill-pouches with the respiratory

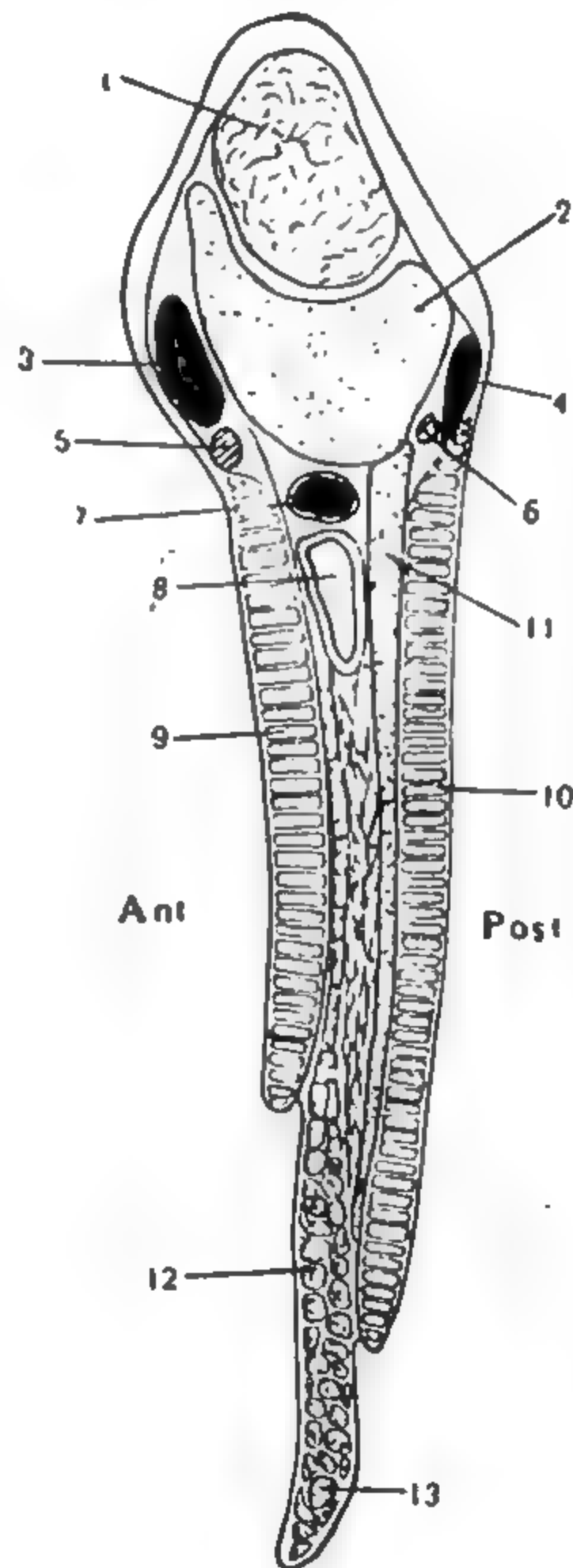
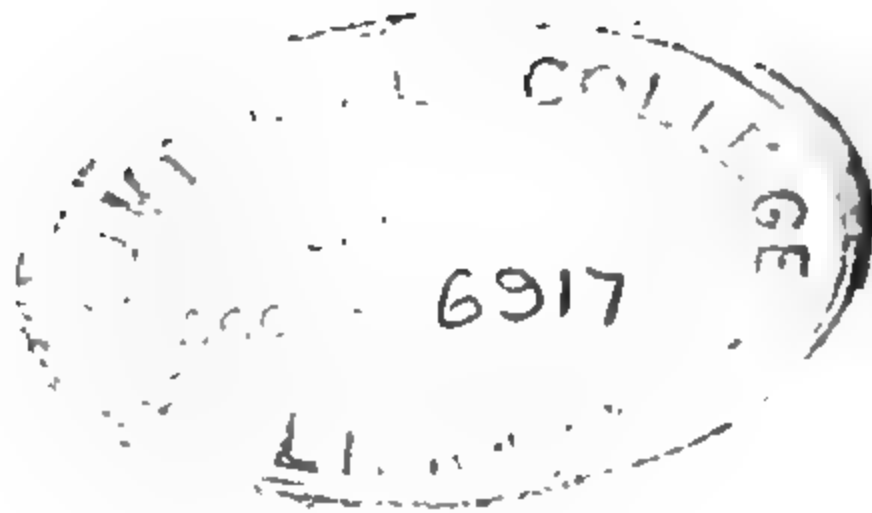


Fig. 62—A horizontal section through a holobranch taken parallel to the branchial lamellae. 1, muscle; 2, epibranchial cartilage; 3, anterior efferent branchial artery; 4, posterior efferent branchial artery; 5, pre-trematic nerve; 6, post-trematic nerve; 7, afferent branchial artery; 8, nutrient vein; 9, anterior gill-lamella; 10, posterior gill-lamella; 11, branchial ray; 12, inter-branchial septum; 13, extra-branchial cartilage. (\times cir, 6)

current contains oxygen dissolved in it. This water is separated from the blood contained within the capillaries of the gill-lamellae merely by the thin and permeable membranous walls of the capillaries; the oxygen of the water passes by endosmosis through the thin capillary walls into the blood, and at the same time the carbon dioxide of the blood passes into the water by a process of exosmosis. The oxygen is conveyed by the blood to all parts of the body, while carbon dioxide brought to the gills in the venous blood is eliminated by the water of the outgoing respiratory current. As the blood makes a complete circuit in the capillaries of the gills in a very short time, it is evident that the exchange of gases also takes place very quickly.



CHAPTER VIII

THE BLOOD-VASCULAR SYSTEM

The structures concerned with blood-circulation are: (a) a four-chambered *heart*, which is the organ of propulsion of the venous blood to the gills, (b), the *arteries*¹ which carry blood from the heart to the gills and from the gills to all parts of the body, and (c) the *veins*¹ which return the blood from the body to the heart.

THE HEART AND THE AFFERENT BRANCHIAL ARTERIES.

The heart is a dorso-ventrally bent muscular tube consisting of four chambers: the *sinus venosus*, the *atrium*, the *ventricle* and the *conus arteriosus* (figs. 63 and 64).

The *sinus venosus* is a triangular thin-walled chamber elongated transversely and lying along the base of the pericardial cavity. Two large veins, the *ducti Cuvieri*, enter the sinus venosus laterally, one on each side, while two *hepatic sinuses* open into it posteriorly near the median line (fig. 68). The sinus venosus opens anteriorly into the atrium through the *sinu-atrial aperture*, guarded by a pair of membranous valves which prevent a backward flow of the blood. The *atrium* (*auricle*) is a large triangular sac which has thicker walls than those of the sinus venosus and is situated in front of the sinus venosus and dorsally to the ventricle. The sides of the atrium projecting on either side of the ventricle give it a characteristic ear-like or auricular appearance. It communicates with the ventricle through the *atrio-ventricular aperture* guarded by a bilabiate valve (fig. 63). The sinus venosus and atrium have elastic rather than muscular walls and form the *receiving chambers* for the venous blood from all parts of the body.

The *ventricle* is the most prominent chamber supported ventrally by the coracoid cartilages; it has a very thick muscular wall, the inner surface of which is produced into numerous muscular strands, giving this surface a spongy texture. The *conus arteriosus* (fig. 63) is a stout muscular tube extending from the ventricle to the anterior apex of the pericardial cavity; its inner wall is provided with two

¹ As far as possible, the nomenclature of blood-vessels adopted here is as given by C.H. O'Donoghue in his admirable memoir on the "Blood-vascular system of the Spiny Dogfish". Trans. Roy. Soc. Edin., vol. 55, 1928.

transverse rows of semi-lunar valves, each row containing three valves, one dorsal and two ventro-lateral in position; in addition, there is always a small accessory valve on either side of each dorsal valve. Fine tendinous threads extend from the free ends of the valves anteriorly and posteriorly to the ventricular wall to hold the valves in position. The conus arteriosus is continued forward through the wall of the pericardium as the *ventral aorta*. The ventricle and the conus constitute the *forwarding pump* for the blood.

The *ventral aorta* (fig. 64) extends along the ventral surface of the pharynx right up to the posterior border of the hyoid arch, where it bifurcates into two branches, the *innominate arteries*, each of which again divides into two, the *first* and *second afferent branchial arteries*. The first afferent runs along the posterior border of the hyoid arch and supplies branches to all the gill-lamellae of the hyoidean demi-branch. The second afferent follows a similar course along the first branchial arch, supplying branches to both the anterior and posterior gill-lamellae along its whole length. The third, fourth, and fifth afferent arteries arise from the ventral aorta almost equidistant from one another and run along the outer borders of the second, third and fourth branchial arches. Each afferent branchial arises by its own separate opening from the ventral aorta, except the hind-most pair of branchial arteries which arise together through a common median opening (fig. 63).

The function of the heart in a fish is to receive the non-aerated blood from all parts of the body and pump it to the gills for aeration. Since the blood passes through the heart only once in its complete circuit round the body, it is obvious that there should be sufficient pressure in the heart to force the blood through the gills and thence to the different organs of the body. This is brought about by the rhythmic contraction of the different parts of the heart in a definite succession and at regular intervals. The heart-beat or contraction starts in the sinus venosus and the blood brought to it from the different parts of the body by the veins is forced into the atrium through the sinu-atrial aperture, the membranous valves guarding this aperture preventing the blood from flowing back into the sinus venosus. The wave of contraction next spreads over the atrium and drives the blood into the ventricle, where again the return of blood into the atrium is prevented by the bilabiate valve guarding the atrio-ventricular aperture. Then follows the contraction of the ventricle forcing the blood into the conus arteriosus. As the wave of contraction passes from the ventricle to the conus, any return of the blood into the ventricle is prevented by the two rows of semi-lunar valves in the conus arteriosus (fig. 63). From the conus the

blood passes into the ventral aorta and thence to the afferent branchial arteries which break up into capillaries in the gill-lamellae where the blood is oxygenated. In fishes the heart contains only venous blood which it pumps into the gills: such a heart is described as a *venous* or "*branchial*" heart.

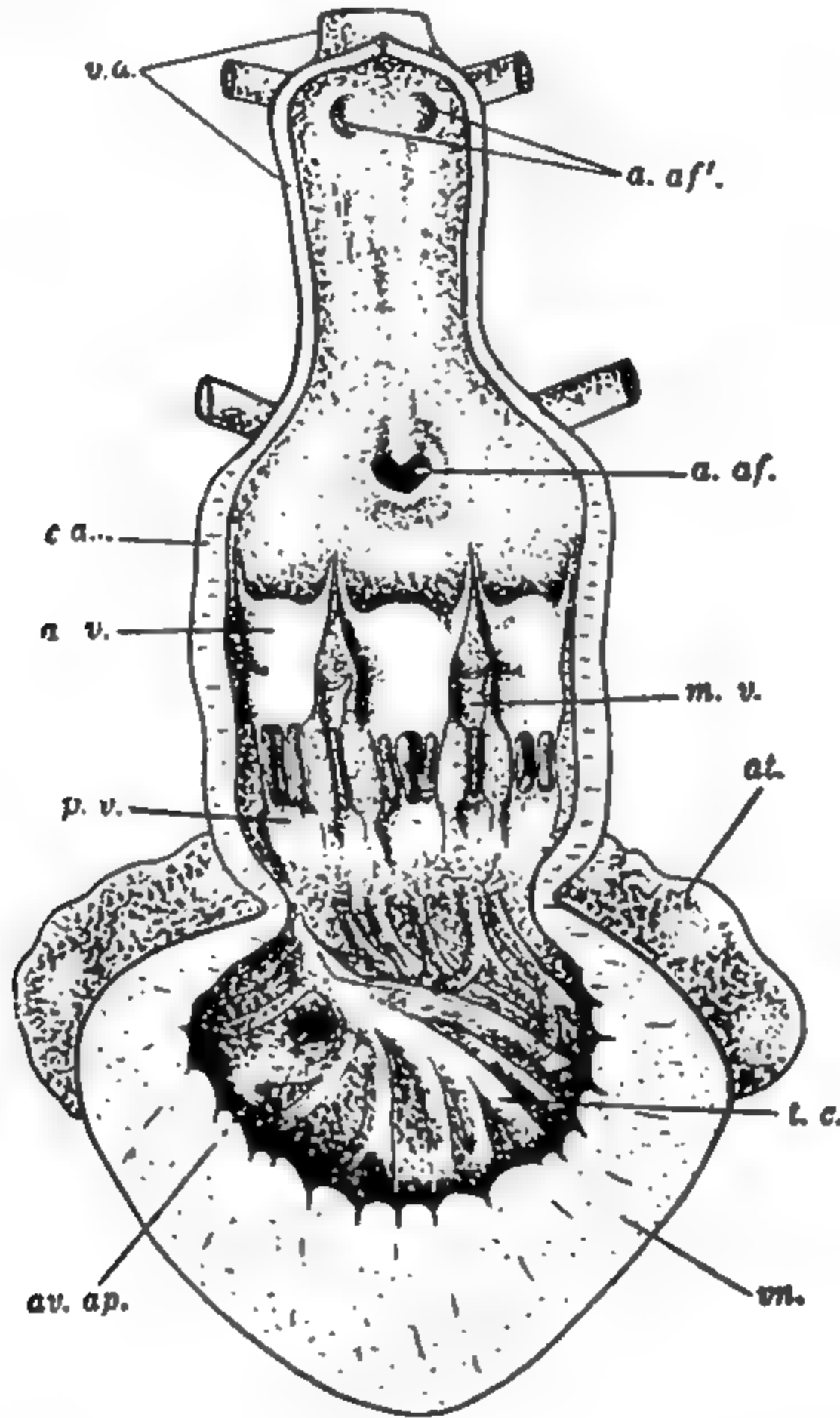


Fig. 63—The heart of *Scoliodon* dissected from the ventral surface. *a.af.*, median aperture of the fifth pair of afferent arteries; *a.af.l.*, paired apertures of the fourth afferent arteries; *a.v.*, anterior row of semi-lunar valves; *at.*, atrium or auricle; *av. ap.*, atrio-ventricular aperture; *c. a.*, conus arteriosus; *m. v.*, miniature accessory valve; *p. v.*, posterior row of semi-lunar valves; *l.c.*, cordae-tendinae; *v. a.*, ventral aorta; *m.*, muscular wall of the ventricle. (\times cir. 5).

THE EFFERENT BRANCHIAL ARTERIES.

The blood from the capillaries of the gills is collected by a series of blood-vessels called the *efferent branchial arteries*. There are

nine efferent branchial vessels on each side (*fig. 64, ef1-ef9*), running along the anterior and posterior borders of the five gill-clefts. Of these the first eight join together in pairs to form a series of *four* complete *collector loops* around the first four gill-clefts: but as the fifth gill-pouch bears only a demibranch on its anterior wall, there is no complete loop round the fifth cleft, and the blood collected by the ninth efferent vessel from this demibranch is conveyed to the fourth loop by a longitudinal connective. The four loops are connected with one another by short *longitudinal connectives* which run within their interbranchial septa and connect the posterior efferent of a gill-cleft with the anterior efferent of the next cleft behind; the loops are further connected with one another by a network of *longitudinal commissural vessels* (*lateral hypobranchial chain*) between their ventral extremities. The posterior efferent artery of each loop is much larger than the anterior and receives the major portion of the blood from each gill.

Each of the four efferent branchial loops is continued into an *epibranchial artery* which runs backward and inward to the mid-dorsal line; these four pairs of epibranchials unite to form the median *dorsal aorta* (*fig. 64*), the half-loop (*ef9*) of the ninth efferent branchial, having no epibranchial of its own, joins the eighth efferent branchial.

THE ARTERIES OF THE HEAD.

The head receives its blood-supply directly from the first efferent branchial (*hyoidean efferent*) and a small part from the anterior end of the dorsal aorta, unlike the rest of the body which is supplied entirely by branches from the dorsal aorta.

The arteries of the head (*fig. 64*) originate from the *first* or *hyoidean efferent* (*ef1*) and consist of three pairs of large arteries: (i) the external carotid, (ii) the afferent spiracular, and (iii) the hyoidean epibranchial, which receives a branch from the anterior end of the dorsal aorta.

(i) The *external carotid artery* (*e.c.*) arises at the antero-ventral corner of the first collector loop and travels along the outer surface of the hyoid arch, dividing into two branches, the ventral mandibular and superficial hyoid arteries. The *ventral mandibular* (*v.m.a.*) runs forward and outward, gives off small branches to the coraco-mandibular muscles and continues along the inner surface of the lower jaw to supply its muscles. The *superficial hyoid* (*su.h.*) passes a little inward, gives off an *anterior thyroid branch* and then curves towards the ventral side to supply the second ventral constrictor muscle and the skin, and the sub-cutaneous tissue over the ventral part of the hyoid arch. (ii) The *afferent spiracular artery* (*af.s.*) arises at about the

middle of the hyoidean efferent and runs forward on the outer side of the hyomandibular and epi-hyal cartilages, and then bends inward surrounding the spiracle; it then continues forward and inward as the *spiracular epibranchial artery* (*sp.ep.*) across the floor of the orbit, passes over the branches of the stapedia artery and enters the cranial cavity through a small foramen (fig. 49; 4). Just before entering the cranial cavity it gives off the *great ophthalmic artery* (*g.o.*) to the eye-ball. Within the cranium it unites immediately with a branch of the internal carotid to form the *cerebral artery* which is a short vessel dividing immediately into *anterior* and *posterior cerebral arteries*. The *anterior cerebral* passes along the outer border of the fore-brain which it supplies and then divides into branches supplying the olfactory lobe of the brain and the olfactory sac; the *posterior cerebral* supplies branches to the different parts of the brain behind the diencephalon and passing ventrally to the medulla oblongata unites with its fellow of the opposite side to form a median ventral artery, the *basilaris* (*ba.a.*), which runs backward along the whole length of the ventral surface of the spinal cord as the *spinalis* or *myelonal artery*. (iii) The *hyoidean epibranchial artery* (*h.e.*) arises close to the dorsal end of the hyoidean efferent and runs forward and inward along a canal in the roof of the buccal cavity to the posterior border of the orbit, where it is joined by an anterior branch of the dorsal aorta (*d.a.*) and immediately divides into two branches, the *stapedial* and the *internal carotid*. The *stapedial artery* (*st. a.*) enters the orbit through a foramen (fig. 48; 24C) in the floor of the cranium and runs forward and outward across the orbit, where it gives off a large vessel, the *inferior orbital artery* (*i.o.*), supplying several branches to the six eye-muscles and the superficial tissue in the region above the auditory capsule. The main branch of the *stapedial* runs forward as the *superior orbital* (*su.o.*) to the anterior boundary of the orbit where it gives off a large *buccal artery* and continues forward to the snout as the *maxillo-nasal*. The *buccal artery* (*bu.a.*) runs far backward along the upper border of the orbit and finally ends in the muscles of the lower jaw. The *maxillo-nasal* (*m.n.*) leaves the orbit and runs along the edge of the upper jaw, sends a *nasal artery* (*n.a.*) to the olfactory sac and several *maxillary branches* to the muscles of the upper jaw, and then passes along the mid-ventral line as the *rostral artery* (*ro.a.*) to supply the region of the rostrum. The *internal carotid* (*i.c.*) passes inward along a groove in the roof of the buccal cavity and enters the cranium through a foramen (fig. 48; 24B), lying mesially to the foramen for the stapedial; within the cranial cavity it divides into two branches one of which unites with its fellow of the opposite side, while the other unites with the stapedial to form the anterior and posterior cerebral arteries.

THE HYPOBRANCHIAL BLOOD-PLEXUS.

It is a complex system of small blood-vessels on the ventral wall of the pharynx. A network of slender arteries arises from the ventral ends of the efferent branchial loops, and forms a *lateral hypobranchial chain* (*l.h.*) connecting the ventral ends of all the four efferent branchial loops (fig. 64). Four *commissural vessels* (*c.v.*) arise from these lateral hypobranchials and pass towards the mid-ventral line to meet on the ventral wall of the ventral aorta and form a pair of *median hypobranchials*. The first commissural is given off at the level of the first efferent loop, the second at the level of the third loop, the third at the level of the fourth loop, and the fourth at the level of the ninth efferent branchial (*efg*), there being no commissural at the level of the second efferent loop. The paired median hypobranchials communicate with each other by small transverse vessels, and at their junction with the fourth commissural unite to form a *median coracoid artery* (*m.c.a.*) which runs backward to the beginning of the conus arteriosus, and gives rise to the *coronary artery* (*co.a.*), which is specially well developed in *Scoliodon*. The coronary artery divides into a ventral branch supplying the ventricle and the conus, and two dorso-lateral branches supplying the atrium and the sides of the ventricle. A *pericardial artery*, also given off from the median coracoid, passes backward into the pericardial cavity and immediately divides into two branches which diverge right and left, and supply blood to the dorsal wall of the pericardium. At the anterior end, close to its origin, the pericardial artery gives off the *common epicoracoid artery*, which immediately divides into *right* and *left epicoracoids*.

Fig. 64.—A dorsal view of the afferent arteries and ventral view of the efferent arteries and their branches in *Scoliodon palasorrah*. *a.c.*, anterior cerebral artery; *af.1-af.5*, first to fifth afferent branchial arteries; *af.s.*, afferent spiracular artery; *at.*, atrium; *ba.a.*, basilar artery; *b.b.*, bucal branch; *br.a.*, branchial artery; *bu.a.*, buccal artery; *c.a.*, conus arteriosus; *ce.a.*, cerebral artery; *cl.1-cl.5*, first to fifth branchial clefts; *c.m.a.*, coeliaco-mesenteric artery; *co.a.*, coronary artery; *cr.*, wall of cranium; *c.v.*, commissural vessel; *d.a.*, dorsal aorta; *d.a.1*, one of the anterior branches of the dorsal aorta; *e.*, eye; *e.c.*, external carotid; *ef.1-efg*, first to ninth efferent branchial arteries; *ep.1-ep4*, first to fourth epibranchial arteries; *ep.a.*, epicoracoid artery; *for.*, foramen in the pectoral girdle for the branchial artery; *g.o.*, great ophthalmic artery; *h.e.*, hyoidean epibranchial; *i.a.*, innominate artery; *i.c.*, internal carotid artery; *i.o.*, inferior orbital artery; *l.h.*, lateral hypobranchial chain; *m.c.a.*, median coracoid artery; *m.n.*, maxillo-nasal artery; *n.*, nasal aperture; *n.a.*, nasal artery; *ol.s.*, olfactory sac; *p.c.*, posterior cerebral artery; *per.*, pericardial cavity; *p.h.a.*, paired hypobranchial arteries; *ro.a.*, rostral artery; *s.a.*, subclavian artery; *sp.*, spiracle; *sp.ep.*, spiracular epibranchial; *st.a.*, stapedial artery; *su.h.*, superficial hyoid artery; *su.o.*, superior orbital artery; *s.v.*, sinus venosus; *v.a.*, ventral aorta; *v.m.a.*, ventral mandibular artery; *vn.*, ventricle; *vt.a.*, vertebral artery.

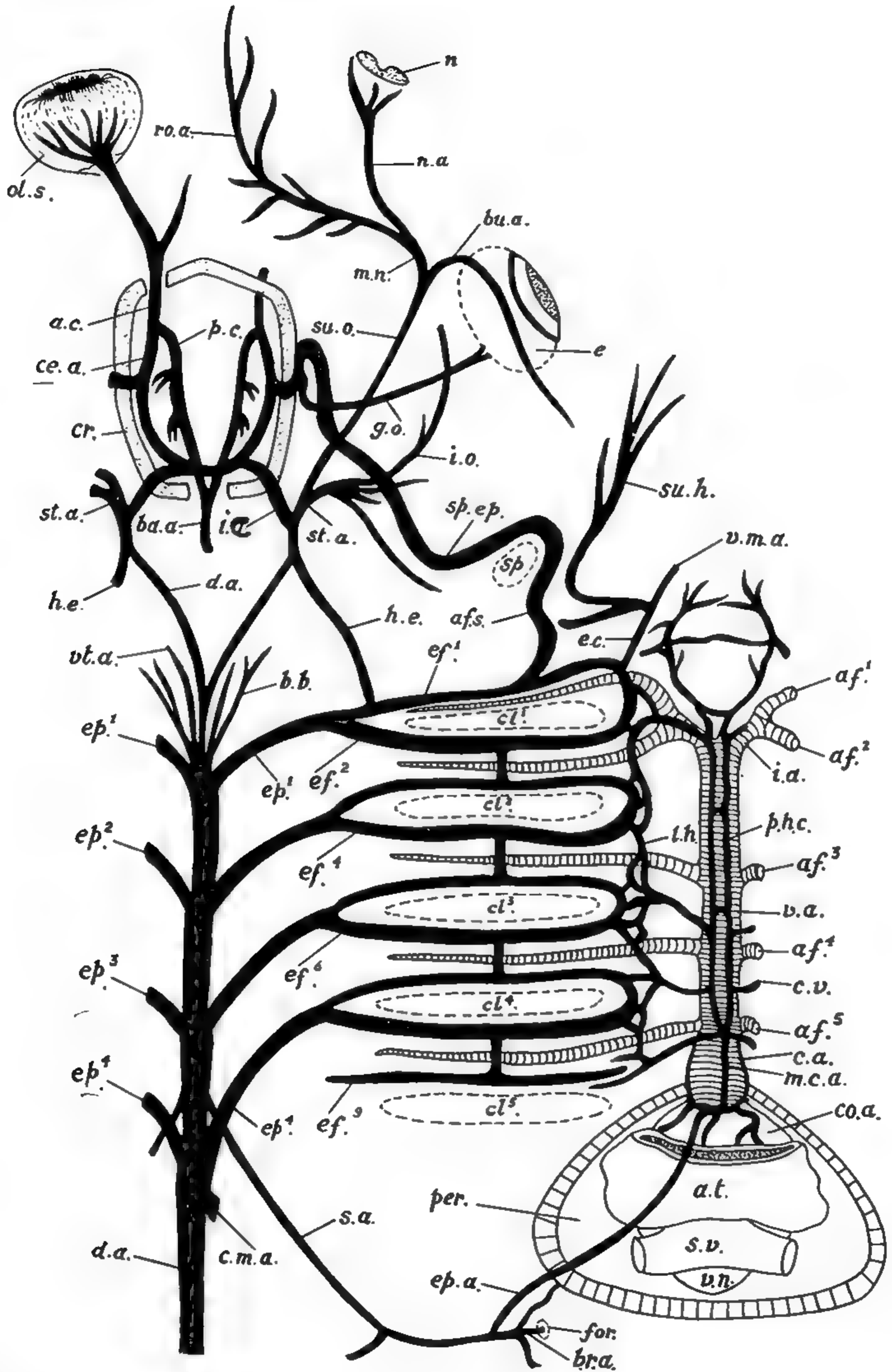


Fig. 64

(*ep.a.*) that run ventrally along the coracoid segment of the pectoral girdle to join the subclavian artery on each side.

THE DORSAL AORTA AND ITS BRANCHES.

The *dorsal aorta* (fig. 64), formed by the union of four pairs of epibranchial arteries, runs backward along the whole length of the body, lying beneath the vertebral column in the trunk, and continuing within the haemal canal of the tail-vertebrae as the *caudal artery*. The dorsal aorta supplies oxygenated blood through its branches to all the structures behind the gills; anteriorly it gives off several small branches to the roof of the buccal cavity (*b.b.*) and the vertebral column (*vt.a.*), while two of its branches run forward and outward to join the hyoidean epibranchial of each side. Further back, it gives off a pair of comparatively small vessels, the *subclavian arteries*, close to the union of the fourth epibranchial arteries. Each subclavian passes backward and outward to the pectoral girdle, unites with the *epicoracoid artery* and divides into: (a) a *brachial artery* which enters the foramen of the pectoral girdle and supplies the pectoral fin, (b) an *anterior lateral* which runs backward along the muscles of the body-wall, and (c) a *dorso-lateral* which passes forward to the dorsal body-muscles.

The *coeliaco-mesenteric* is a large unpaired artery arising from the dorsal aorta slightly behind the junction of the fourth pair of epibranchial arteries. It divides into two unequal branches: the smaller *coeliac* and the larger *anterior mesenteric* (fig. 65); the *coeliac artery* divides into an *anterior dorsal gastric* and an *anterior ventral gastric*; the former supplies the dorsal wall of the cardiac stomach and gives off a *hepatic artery* supplying the right and left lobes of the liver; the latter travels obliquely along and supplies the ventral wall of the cardiac stomach. The *anterior mesenteric* gives off a *pancreatic artery* to the pancreas, and then passes backward to the distal end of the pylorus where it divides into an *anterior* and a *posterior intestinal*; the anterior intestinal supplies the dorsal wall of the intestine, and

Fig. 65—The vascular supply of the alimentary canal. ARTERIES: 1, coeliaco-mesenteric; 2, coeliac artery; 3a, anterior dorsal gastric; 4, hepatic; 5, anterior mesenteric; 6, anterior ventral gastric; 7, lieno-gastric; 8a, pancreatic branch of the lieno-gastric; 9, pancreatic branch of the anterior mesenteric; 10a, posterior gastric; 11, splenic; 12, posterior intestinal; 13, posterior mesenteric; 14a, posterior intestinal; 15a, anterior intestinal. *p.g.*, main trunk of the lienogastric artery. VEINS: 3v, anterior gastric; 8v, pancreatic; 10v, posterior gastric; 14v, posterior intestinal; 15v, anterior intestinal; 16 and 17, hepatic portal; 18, lieno-gastric; *int.*, intestine; *l.*, liver; *oes.*, oesophagus; *p.*, pancreas; *p. g.*, posterior gastric; *r.*, rectum; *r. g.*, rectal gland; *sp.*, spleen; *st.*, stomach.

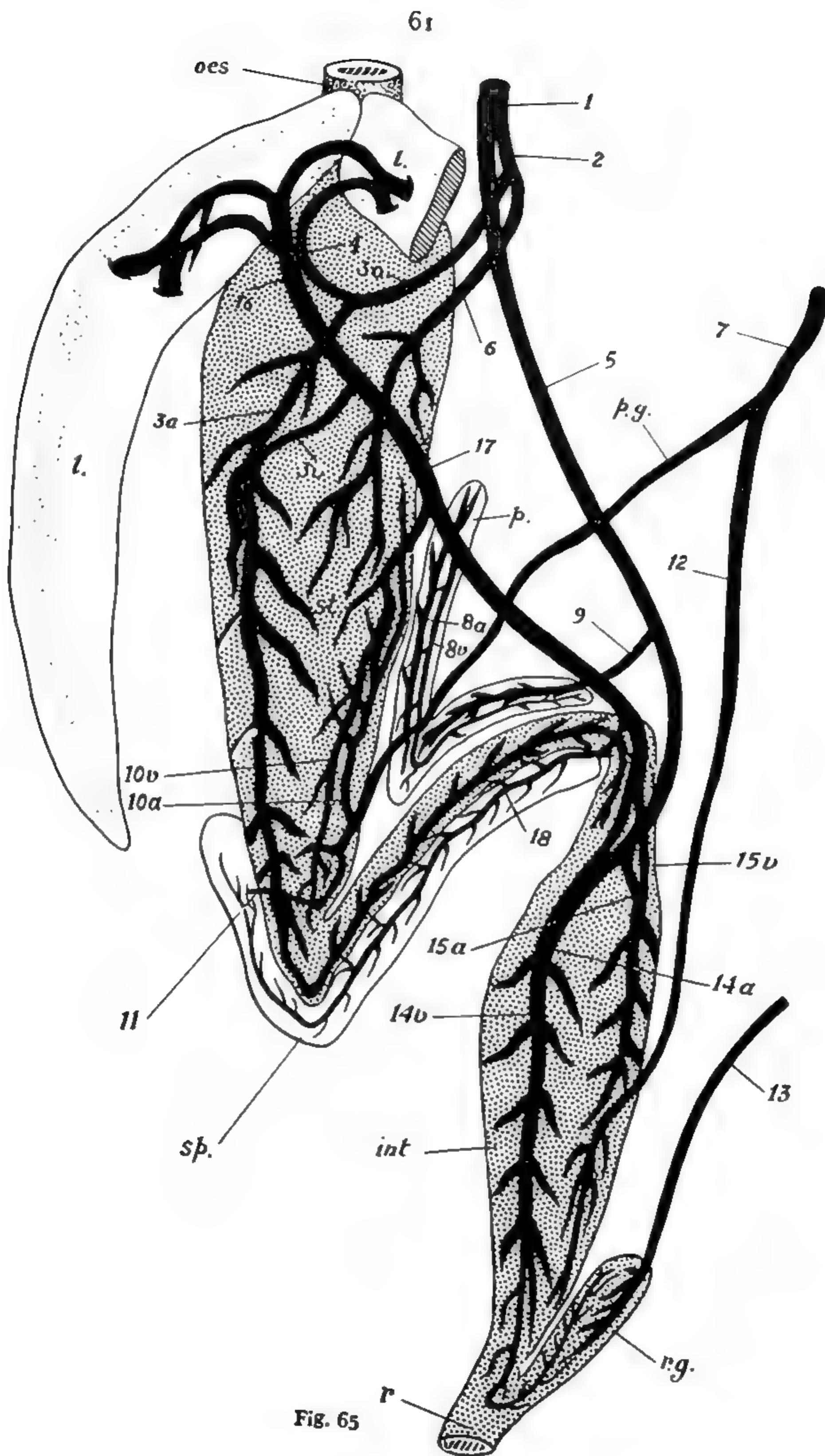


Fig. 65

gives off an *intra-intestinal* which penetrates the wall of the intestine at the level of the beginning of the scroll-valve and runs along the free edge of the valve supplying branches all along its length; while the *posterior intestinal* supplies the ventral wall of the intestine.

The *lieno-gastric* (fig. 65) arises from the dorsal aorta a short distance behind the origin of the coeliaco-mesenteric, and gives off at once the *spermatic* or *ovarian artery* to the testis or ovary. Further along its course it gives off a *posterior intestinal artery* which travels backward and supplies the posterior part of the intestine. The main trunk (*p.g.*) of the lieno-gastric, however, travels to the distal end of the cardiac stomach where it gives off *posterior gastric* to the posterior part of the cardiac stomach and a *splenic artery* to the spleen, besides giving off a few branches to the pancreas. The *posterior mesenteric* is a small artery which supplies the posterior end of the testis and finally ends in the rectal gland.

A series of paired vessels arise from the dorsal aorta all along its length behind the subclavian artery: these are the *parietal arteries*. Each parietal divides typically into two branches, a *dorsal parietal* and a *ventral parietal*. The dorsal parietal passes dorsally around the side of the vertebral column and divides into several branches supplying blood to the thick dorso-lateral muscular bundles, the vertebral column, the spinal cord, and the lateral line canal. The ventral parietal, on the other hand, runs outward to supply the peritoneum and the ventral muscles, besides giving off a *renal branch* in the region of the kidneys. The dorsal fins are supplied by the dorsal parietals. Several pairs of parietals give off branches to the oviduct along the greater part of its length. The *iliacs* are a pair of arteries similar to the parietals; each extends into the pelvic fin as a *femoral artery* and there breaks up into capillaries.

THE VEINS.

The blood distributed to the different parts of the body by the arteries and their branches is collected through capillaries and returned to the heart by the veins. The veins differ in structure from the arteries in possessing thin walls and in forming during their course wide irregular spaces called *sinuses*.

The veins may be considered under the following systems: (i) the *anterior cardinal system* returning blood from the head, (ii) the *posterior cardinal system* draining the kidneys and the dorsal body-wall, (iii) the *sub-intestinal or hepatic portal system* carrying blood from the alimentary canal to the liver, (iv) the *ventral veins* returning blood from the ventral body-wall, the paired fins and the ventral region

of the head, and (v) the *cutaneous system* collecting blood from the integument.

(i) The *anterior cardinal system* (fig. 67) consists of a pair of large vessels, the *internal jugular veins*, which drain blood from the dorsal region of the head and the branchial region. Each internal jugular comprises the *olfactory sinus*, the *orbital sinus*, the *post-orbital sinus* and the *anterior cardinal sinus*. The rostral region is drained by a number of small veins which unite to form the *anterior facial vein* leading into the *olfactory sinus*; this sinus passes through a foramen in the floor of the olfactory capsule into the *orbito-nasal canal* which opens into the orbital sinus. Each *orbital sinus* lies in the orbit beneath the eye-ball and is connected with its fellow of the opposite side by an *inter-orbital vein* lying in the *inter-orbital canal* of the floor of the cranium. The orbital sinus leads into the *anterior cardinal sinus* through the narrow *post-orbital sinus* situated above the auditory capsule. The *anterior cardinal* is a large sinus running backward between the dorsal ends of the gill-pouches and the muscles of the body-wall and entering the *ductus Cuvieri* behind. The anterior cardinal also receives blood from the *hyoidean sinus* which extends obliquely from the mandibular symphysis to the first gill-cleft, where it runs more or less parallel to the cleft ventro-dorsally, and is connected above with the anterior cardinal sinus and below with the inferior jugular sinus. The five *dorsal nutrient branchial sinuses* from the gills also empty their blood into the anterior cardinal sinus by separate openings (fig. 67).

(ii) The *posterior cardinal system* consists of a median caudal vein, two renal portal veins and two large posterior cardinal sinuses. The blood from the tail is collected by the *caudal vein* which traverses the haemal canal of the caudal vertebrae beneath the caudal artery, and receives numerous branches on either side from the myotomes of the tail. On entering the abdominal cavity dorsally to the cloaca, it bifurcates into *right* and *left renal portal veins* which continue forward along the dorso-lateral margins of the kidneys, and branch into numerous sinusoid capillaries within the substance of each kidney. Small *parietal veins* from the body-wall join the renal portal veins all along their length. The blood from the sinusoids of the kidneys is collected by the *renal veins* which join together to form the *posterior cardinal sinuses*.

It will be seen that the blood from the capillaries of the tail does not go directly to the heart, but passes through the sinusoid capillaries of the kidneys where it mingles with the blood brought to these organs by the renal arteries. This system of double capillary circulation is known as a *portal system*. There are two portal

systems in fishes: the renal portal system and the hepatic portal system. Of these two, the renal portal is found only in the lower vertebrates *e.g.*, Pisces and Amphibia, while the hepatic portal system is found in all the vertebrates.

The two *posterior cardinal sinuses* lie close together along the the roof of the abdominal cavity, immediately above the dorsal peritoneum. In the posterior region of the kidneys numerous veins join to form a median *inter-renal vein*, but in the anterior region of the kidneys the right and left posterior cardinal sinuses are distinct and are separated by a median partition. In the region of the oesophagus the posterior cardinals expand into wide thin-walled sacs communicating freely with each other. All along their course they receive parietal veins from the body-wall. Finally, each posterior cardinal opens into the Cuvierian duct by a relatively small aperture, opposite the opening of the anterior cardinal sinus (fig. 68).

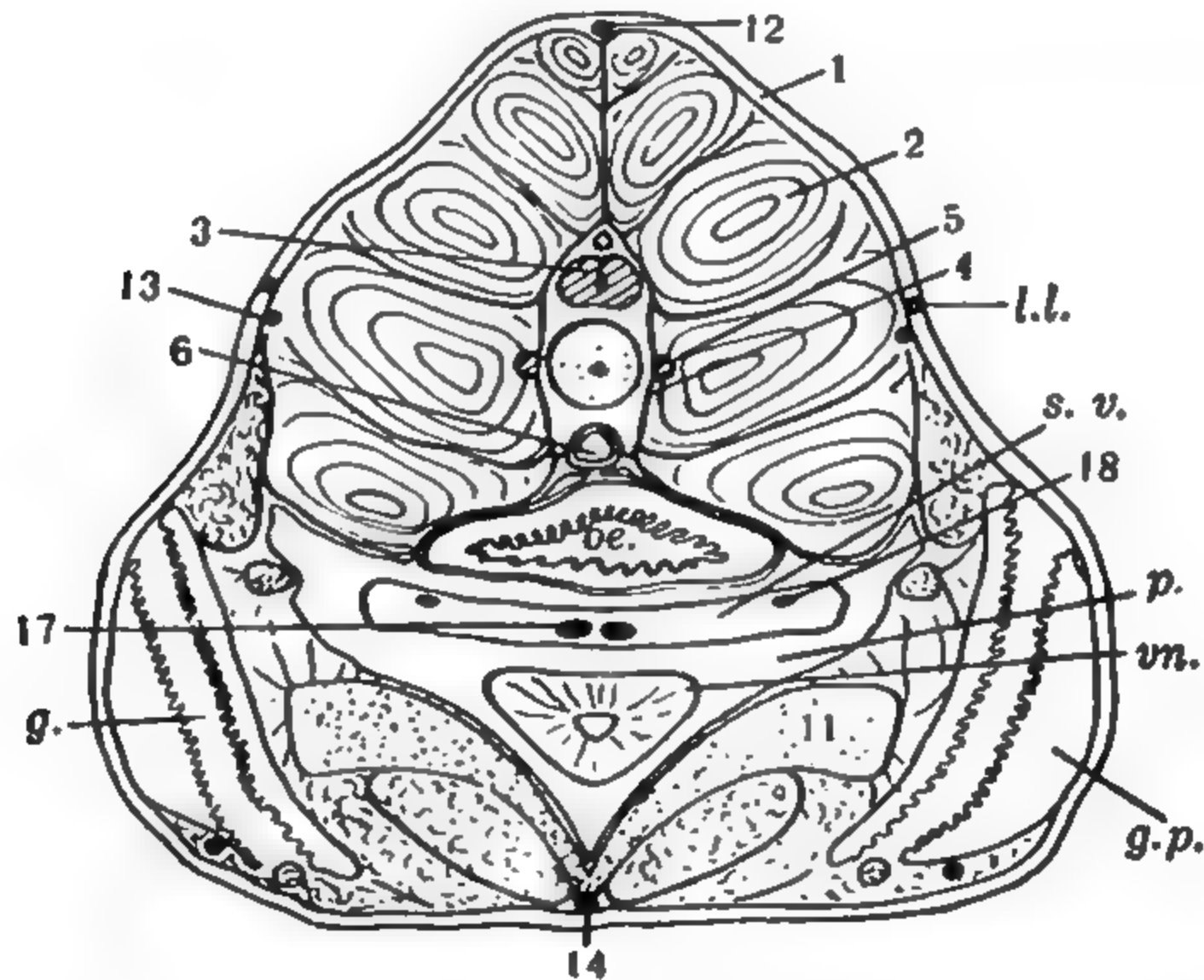


Fig. 66—A transverse section of the shark passing through the oesophagus and pericardial cavity (semi-diagrammatic). 1, integument; 2, myotome; 3, spinal cord; 4, vertebra; 5, spinal nerve; 6, dorsal aorta; 11 coracoid cartilage; 12, dorsal cutaneous vein; 13, lateral cutaneous vein; 14, ventral cutaneous vein; 17, opening of the hepatic sinus; 18, opening of the inferior jugular sinus; g., gill; g. p., gill-pouch; l.l., lateral line canal; oe., oesophagus; p., pericardial cavity; s. v., sinus venosus; vn., ventricle.

(iii) *The sub-intestinal or hepatic portal system.* The blood from the alimentary canal and its associated glands is collected by a number of veins which unite to form the *hepatic portal vein* (fig. 65), beginning near the posterior end of the pyloric stomach by a confluence of the *anterior and posterior intestinal veins*. The large vein so

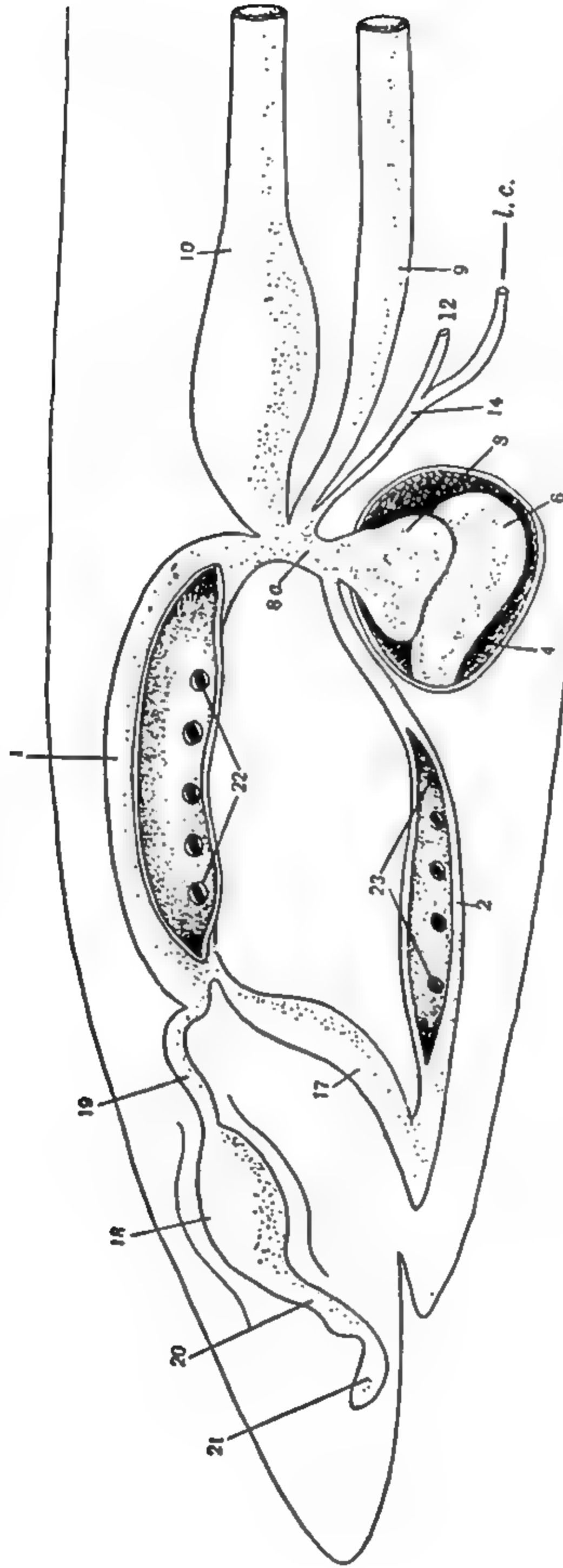


Fig. 67—A side view of the veins of the head and the branchial region. 1, anterior cardinal sinus; 2, inferior jugular sinus; 4, pericardial cavity; 6, atrium; 8, sinus venosus; 8a, ducts Cuvieri; 9, lateral abdominal vein; 10, posterior cardinal sinus; 12, vein from the pectoral fin; 14, brachial vein; 17, hyoid vein; 18, orbital sinus; 19, post-orbital sinus; 20, orbito-nasal sinus; 21, olfactory sinus; 22, openings of the dorsal nutrient sinuses; 23, openings of the ventral nutrient sinuses; *l. c.* lateral cutaneous vein.

formed receives a *lieno-gastric vein*, a little behind the pancreas, and two large veins, the *anterior* and *posterior gastrics*, at the level of the cardiac stomach and then runs forward to divide into two branches which enter the right and left lobes of the liver. The *posterior intestinal* collects blood from the rectal gland and passes forward along the dorsal wall of the intestine; at the anterior end of the intestine it is joined by the *anterior intestinal* formed by the union of the *ventral intestinal* from the ventral wall of the intestine and the *intra-intestinal* from the "scroll-valve". The *lieno-gastric* collects blood from the spleen and the pyloric stomach, while a small *pancreatic vein* drains blood from the pancreas. The *anterior* and *posterior gastrics* collect blood from the cardiac stomach and join the hepatic portal vein in its anterior region. The blood brought to the liver is distributed throughout this organ by a network of capillaries. It is collected by a second set of capillaries which together form two large thin-walled sinuses, the *hepatic sinuses*, traversing the whole length of the of the lobes of the liver and opening anteriorly into the sinus venosus by two small apertures close to the median line opposite the sino-atrial aperture (fig. 68).

(iv) The *ventral veins* consist of two groups: (i) the anterior veins which discharge their blood into the ductus Curieri through the *inferior jugular sinuses*, and (ii) the posterior veins which empty their blood through the *subclavians*.

Each *inferior jugular sinus* commences just in front of the postero-ventral margin of the first gill-cleft and is situated beneath the floor of the buccal cavity and pharynx; it is formed by the union of the *submental sinus* from the lower jaw and the *hyoidean sinus*, and also receives the *ventral nutrients* from the gills. It collects blood from the ventral region of the gill-pouches. Although the dorsal and ventral nutrient sinuses open into the anterior cardinal and inferior jugular sinuses respectively, they are connected with each other within each interbranchial septum. Finally, each inferior jugular sinus opens, on each side, into the *ductus Cuvieri*, which in turn opens into the sinus venosus (figs. 67 and 68). The openings of these sinuses into the Cuvierian sinus are guarded by semi-lunar valves which admit the flow of blood in one direction only, *i.e.* towards the Cuvierian sinus.

The *lateral abdominal veins* are two large vessels, each of which commences at the level of the pelvic girdle by a confluence of a small *cloacal vein* during the wall of the cloaca, and a *femoral vein*, lying dorso-laterally to the basipterygium and draining the greater part of the pelvic fin. Posteriorly the two lateral abdominals are connected with each other by a *commissural vein*, but in front each lateral

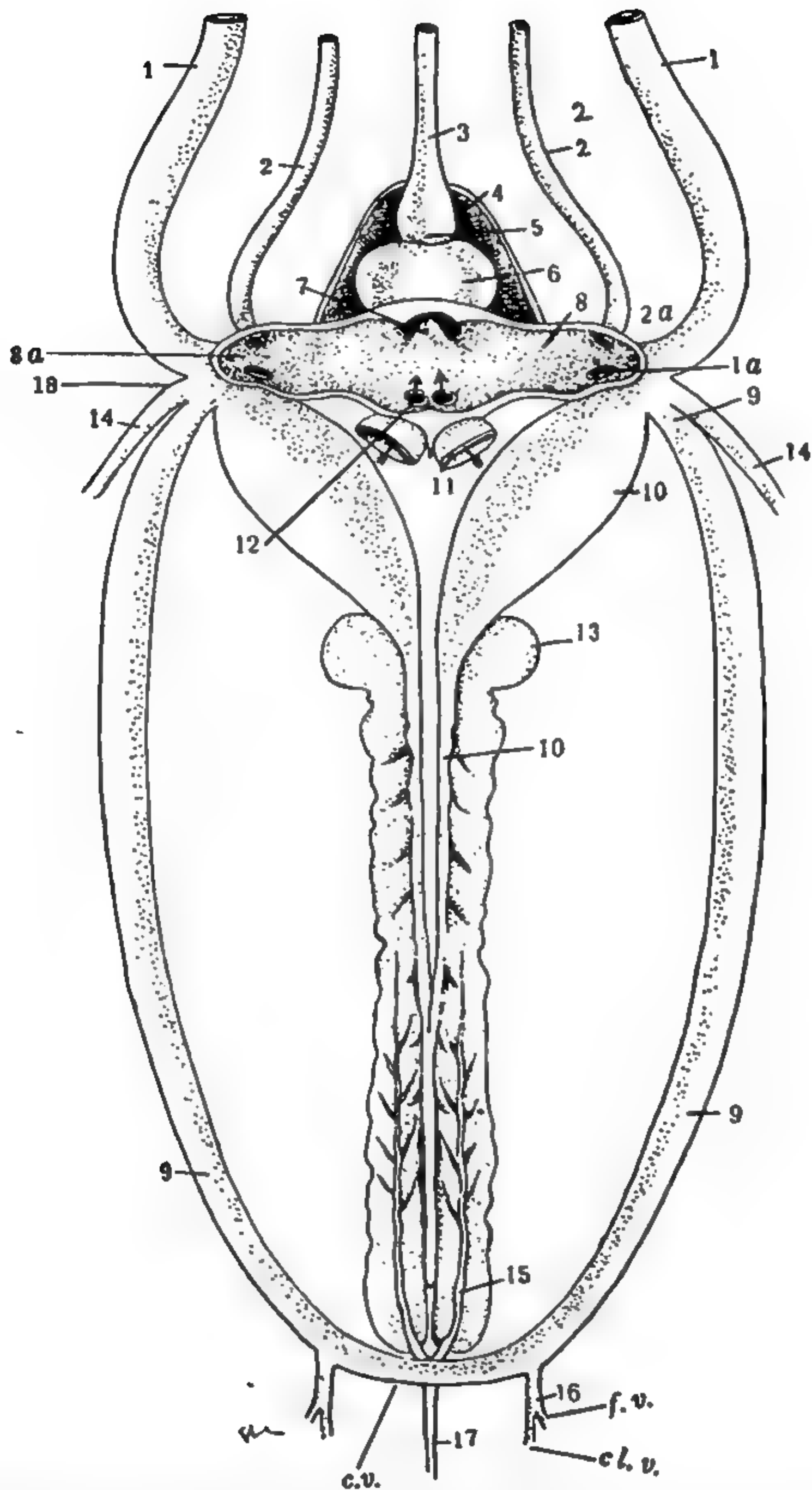


Fig. 68—A ventral view of the veins behind the head. 1, anterior cardinal sinus; 1a, opening of the anterior cardinal sinus into the head. 2, inferior jugular sinus; 2a, opening of the inferior jugular sinus into the ductus Cuvieri; 3, ventral aorta; 4, pericardial cavity; 5, conus arteriosus; 6, atrium; 7, sinu-atrial aperture; 8, sinus venosus; 8a, ductus Cuvieri; 9, lateral abdominal vein; 10, post-venosus; 11, hepatic sinus; 12, opening of the hepatic sinus into the sinus venosus; 13, kidney; 14, brachial vein; 15, renal portal vein; 16, iliac vein; 17, caudal vein; 18, subclavian vein; *c. v.*, commissural vein; *cl. v.*, cloacal vein; *f. v.*, femoral vein.

abdominal remains embedded in the abdominal wall just outside the peritoneum, and runs almost straight forward in the latero-ventral line right up to the pectoral region, where it joins the *brachial vein* to form the large *subclavian vein* which enters the ductus Cuvieri on each side.

The *brachial vein* (fig. 60) is formed at the base of the pectoral fin by the union of two branches draining venous blood from the fin and the body-wall of this region. Each brachial vein also receives a *lateral cutaneous vein*.

(v) The *cutaneous system* consists of a dorsal, a ventral, and two paired lateral veins, which are best seen in transverse sections of the body and tail regions (figs. 60 and 66). The *dorsal cutaneous vein* runs beneath the skin along the mid-dorsal line and collects blood from the skin of the dorsal side; it empties its blood through several branches into the posterior cardinal sinus, the caudal and the lateral cutaneous veins. The *ventral cutaneous* runs along the mid-ventral line beneath the skin, and joins the lateral abdominal in front and the cloacal vein behind. The *lateral cutaneous* runs along each side just beneath the lateral line canal, while the *inferior lateral cutaneous* (fig. 60; 13) runs parallel to the lateral cutaneous but ventrally to it, and joins the latter near the anterior end of the pectoral fin. Each lateral cutaneous empties its blood into the brachial vein in front (fig. 67).

PHYSIOLOGY OF THE BLOOD-VASCULAR SYSTEM.

The blood-vascular system serves for the transport of various substances within the body. Food, water and oxygen are carried by the circulating blood to each living cell of the body, while waste-products, like carbon dioxide and nitrogenous excretions, are removed from every part of the body and taken to the gills, kidney and skin for elimination. The circulatory fluids are the blood and the lymph, each consisting of a liquid portion, the *plasma*, in which float small microscopic *corpuscles*. The plasma is colourless, while the corpuscles are of two kinds: the *erythrocytes* or coloured corpuscles, which give red colour to the blood, and the *leucocytes* or colourless corpuscles. In the lymph only the leucocytes are present, while the blood contains both kinds of corpuscles. The *erythrocytes* are oval nucleated bodies, containing a compound of iron, the *haemoglobin*, which readily combines with oxygen. The erythrocytes are, therefore, oxygen-carriers in the blood and are directly concerned with its respiratory function. The leucocytes, on the other hand, are capable

of amoeboid movements, and some of them have power to engulf foreign bodies in the blood and thus aid in combating pathogenic organisms: hence they are also called *phagocytes*. Absorption of nutritive substances, specially fats, is another function attributed to the leucocytes. The *plasma* contains dissolved food materials, waste products and hormones, besides a few other chemical substances.

The blood, body-fluid and tissues of marine elasmobranchs are characterized by their high urea content (2.0 to 2.5 per cent): this is brought about, firstly, by the relative impermeability of gills and integument to urea which is not allowed to escape to the exterior through these organs, and, secondly, by the development of a special urea-absorbing segment in the urinary tubules (nephrons) of elasmobranch kidneys, which reabsorbs urea from the glomerular filtrate as it passes down the urinary tubules. By virtue of this physiological uraemia, elasmobranchs maintain a slightly higher osmotic pressure than that of sea water and are thus able to absorb a small quantity of water for the formation of an isotonic or hypotonic urine. Another substance called trimethylamine oxide is also actively reabsorbed from the glomerular filtrate, and imparts about a quarter as much osmotic pressure as urea does.

The retention of urea by elasmobranchs is apparently an archaic biochemical habit acquired early in elasmobranch evolution for osmotic regulation in sea-water. During their long stay in the sea the tissues of elasmobranchs have become so accustomed to uraemia that the heart of even a fresh-water elasmobranch of to-day is unable to beat in the absence of urea.

CHAPTER IX

THE NERVOUS SYSTEM

The nervous system consists of two parts: (a) the *central nervous system* including the brain and the spinal cord, and (b) the *peripheral nervous system* comprising the cranial and spinal nerves, and the autonomic nervous system. The central nervous system is essentially tubular and encloses a narrow *central canal* within the spinal cord which widens out anteriorly to form the *ventricles* of the brain.

(a) THE CENTRAL NERVOUS SYSTEM

The brain is divided into a *fore-brain*, a *mid-brain* and a *hind-brain*. The fore-brain includes the *cerebrum* and the *diencephalon*, the mid-brain forms the two *optic lobes*, while the hind-brain comprises the *cerebellum* and the *medulla oblongata*.

The *cerebrum* (fig. 69) is an undivided massive structure with no median groove to separate it into right and left cerebral hemispheres. From either side of its anterior end arises a stout stalk, the *olfactory tract* or *peduncle*, which travels forward and slightly outward and ends into a large bilobed mass, the *olfactory lobe*, closely applied to the olfactory sac of its own side. The dorsal surface of the cerebrum is quite smooth, but on its mid-ventral surface there is a small opening, called the *neuropore* (fig. 70), through which emerge a pair of delicate nerves, the *terminal* or *pre-olfactory nerves*. Each of these nerves bears a ganglion along its course and runs alongside the olfactory tract of its own side to innervate the mucous membrane of the olfactory sac. The cerebrum is continued behind into the narrow *diencephalon* which is extremely short and is completely hidden by the forward prolongation of the cerebellum. The roof of the diencephalon is extremely thin and membranous, being non-nervous in character, but it contains numerous blood-vessels forming the *anterior choroid plexus*. A long slender process called the *pineal body* (fig. 69), arises from the hinder portion of the roof and runs forward and upward to the membrane covering the anterior fontanelle of the skull. The floor of the diencephalon gives off a hollow outgrowth, the *infundibulum*, which projects downward and backward.

Close to the infundibulum lie two thick-walled oval sacs, the *lobi inferiores*, the distal ends of which are continued into a pair of glandular sacs, the *sacci vasculosi* (fig. 70), having extremely thin walls. A median outgrowth derived from the roof of the buccal cavity,

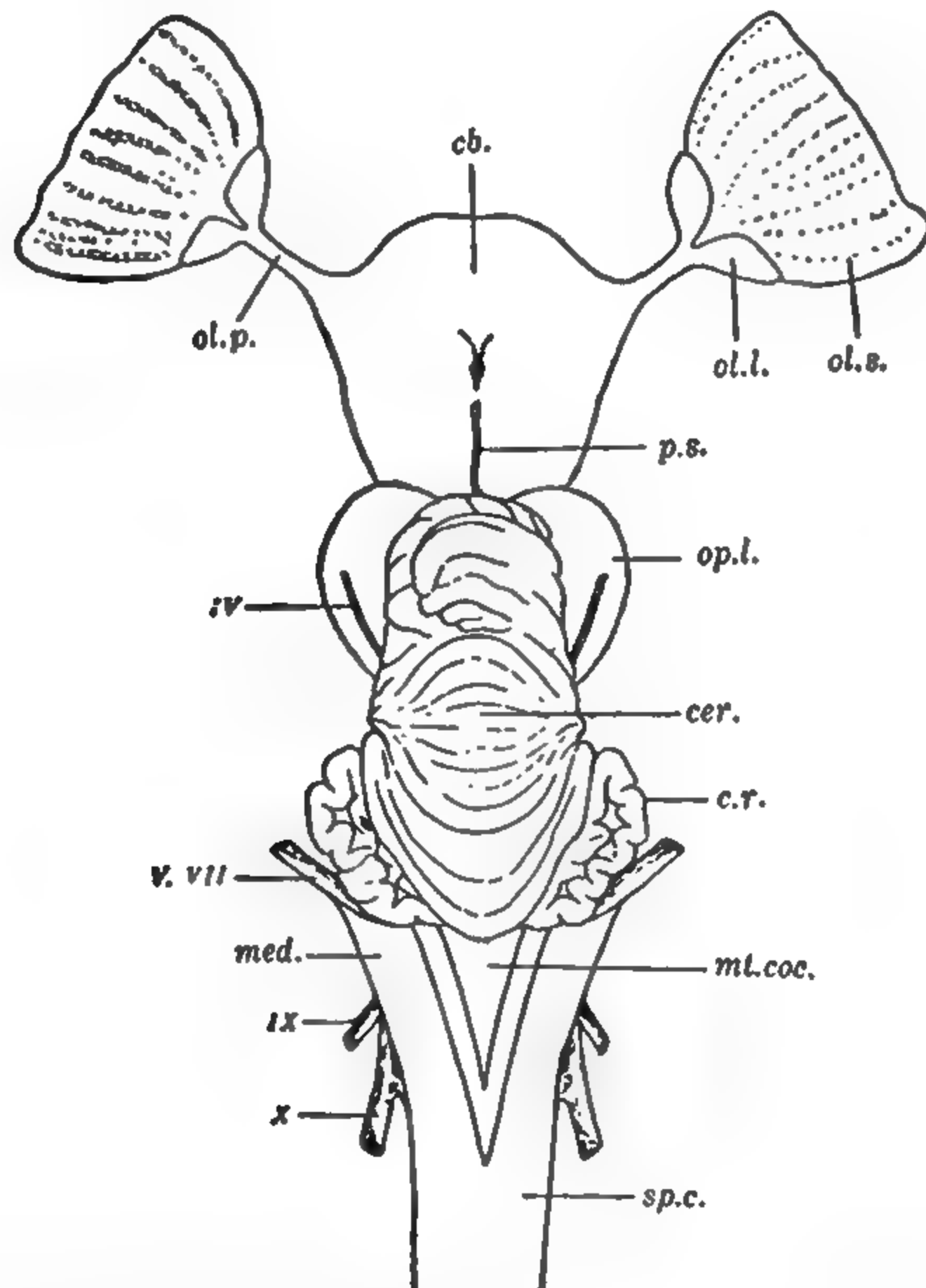


Fig. 69—A dorsal view of the brain. *cb.*, cerebrum; *cer.*, cerebellum; *cr.*, corpora restiformia; *med.*, medulla oblongata; *ol. l.*, olfactory lobe; *ol. p.*, olfactory peduncle; *ol. s.*, olfactory sac; *op. l.*, optic lobe; *p. s.*, pineal stalk; *sp. c.*, spinal cord; *IV* pathetic; nerve; *V, VII*, trigeminal and facial nerves; *IX*, glossopharyngeal nerve; *X*, vagus nerve. (\times cir. $2\frac{1}{2}$).

called the *hypophysis*¹, joins the distal end of the infundibulum. In front of the infundibulum lies the *optic chiasma* formed by the decussation of the fibres of the two *optic nerves*.

¹ In higher vertebrates the infundibulum and the hypophysis are intimately fused together to form the *pituitary body*.

The mid-brain consists of two rounded swellings, the *optic lobes*, into which the fibres of the optic nerves terminate. The optic lobes are almost completely covered over dorsally by the cerebellum and ventrally by the infundibular outgrowths, while their sides are enlarged by the presence of longitudinal nerve-tracts. The *third cranial nerve* arises from the floor of the mid-brain, while the *fourth*

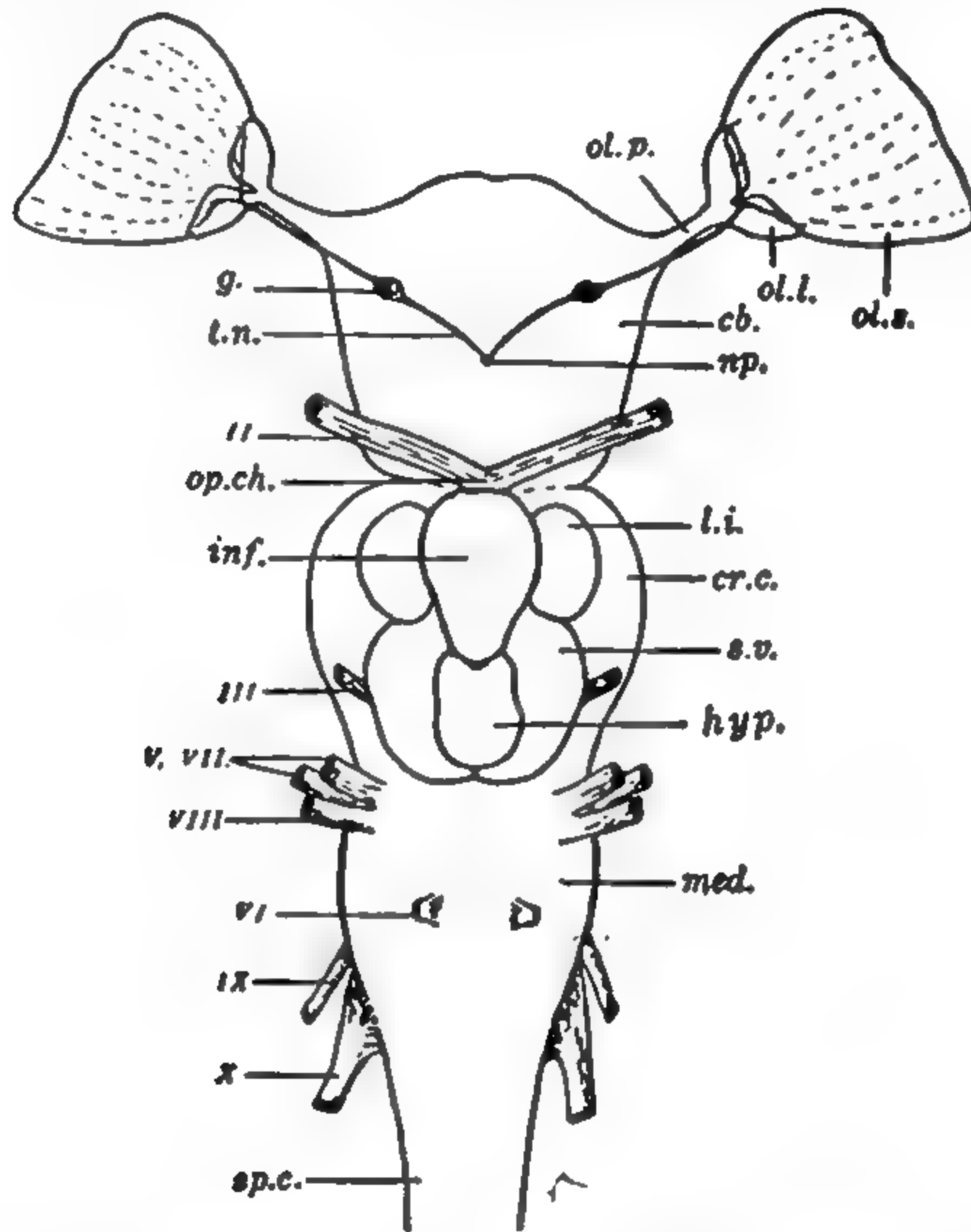


Fig. 70—A ventral view of the brain. *cb.*, cerebrum; *cr. c.*, crura cerebri; *g.*, ganglion of the terminal nerve; *hyp.*, hypophysis; *inf.*, infundibulum; *l. i.*, lobi inferiores; *med.*, medulla oblongata; *np.*, neuropore; *ol. l.*, olfactory lobe; *ol. p.*, olfactory peduncle; *ol. s.*, olfactory sac; *op. ch.*, optic chiasma; *s.v.*, saccus vasculosus; *sp. c.*, spinal cord; *t. n.*, terminal nerve; *II* optic nerve; *III*, oculomotor nerve; *V*, *VII.*, trigeminal and facial nerves; *VI*, abducens nerve; *VIII*, auditory nerve; *IX*, glosso-pharyngeal nerve; *X*, vagus nerve. (\times cir 2 1/2).

cranial nerve arises from the roof between the optic lobes and the cerebellum.

The *cerebellum* is well developed and extends in front up to the cerebrum and overhangs the medulla oblongata behind. It is rhomboid in shape, and its dorsal surface is thrown into numerous

irregular convolutions. Two deep transverse furrows divide the cerebellum into three lobes, while in some forms there is a third median longitudinal furrow dividing it into right and left halves. The *medulla oblongata* is triangular in shape and forms the posterior region of the brain. From its anterior end arise a pair of hollow outgrowths, the *corpora restiformia*, which lie on the dorso-lateral aspects of the medulla and are slightly overlapped by the cerebellum; their walls are thin and, in young forms, greatly convoluted, but in the adult the convolutions are not so marked. A band of nervous tissue lying just behind the cerebellum connects together the corpora

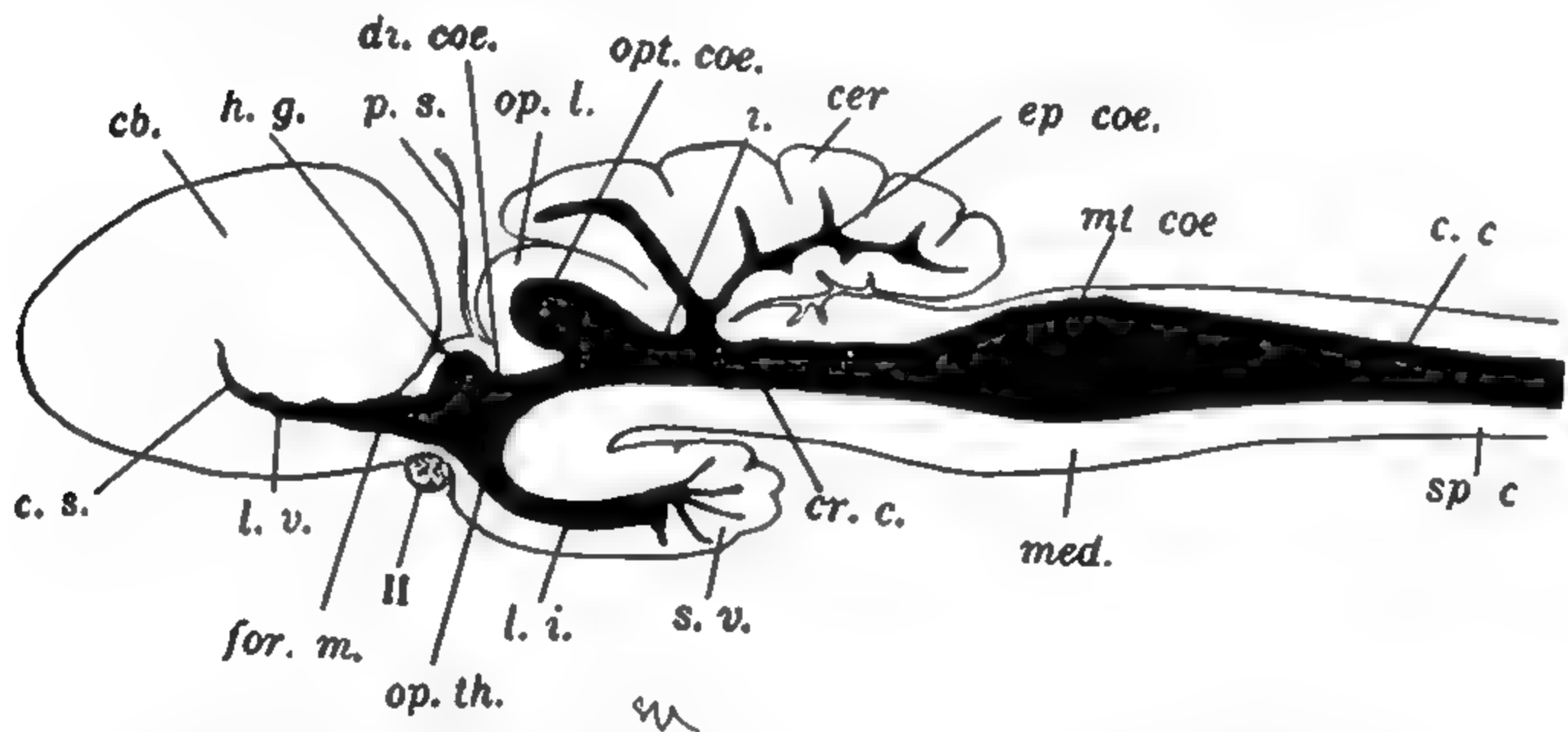


Fig. 71—A vertical longitudinal section of the brain (semi-diagrammatic). *cb.*, cerebrum; *c. c.*, central canal; *c. s.*, corpora striata; *cer.*, cerebellum; *cr. c.*, crura cerebri; *di. coe.*, diacoele; *ep. coe.*, epicoele; *for. m.*, foramen of Monro; *h. g.*, habenular ganglion; *i.*, iter; *l. i.*, lobi inferiores; *l. v.*, lateral ventricle; *med.*, medulla oblongata; *mt. coe.*, metacoele; *op. l.*, optic lobe; *opt. coe.*, optocoele; *op. th.*, optic thalami; *p. s.*, pineal stalk; *s. v.*, saccus vasculosus; *sp. c.*, spinal cord; *II*, optic nerve.

restiformia of the two sides. The floor and sides of the medulla are thick, while the roof is extremely thin and non-nervous and bears the *posterior choroid plexus*. The fifth, seventh and eighth cranial nerves arise from the anterior part of the medulla below the corpora restiformia, the sixth arises from the ventral surface, while the ninth and tenth arise from the sides of the posterior region of the medulla.

A horizontal section through the brain (fig. 72) shows the narrow *central canal* of the spinal cord expanding into a wide triangular chamber, the *fourth ventricle*, the sides and floor of which are greatly thickened by the longitudinal nerve-tracts connecting

the spinal cord with the brain. The fourth ventricle is continued in front into the *iter* or *aqueductus Sylvii* which is very much wider than that of the higher vertebrates and communicates with the cavity of the cerebellum (*epicoele*) above and the *optocoeles* on the two sides, while it is continued in front into the *diacoele* or the *third ventricle* of the diencephalon. The floor of the iter is traversed by two longi-

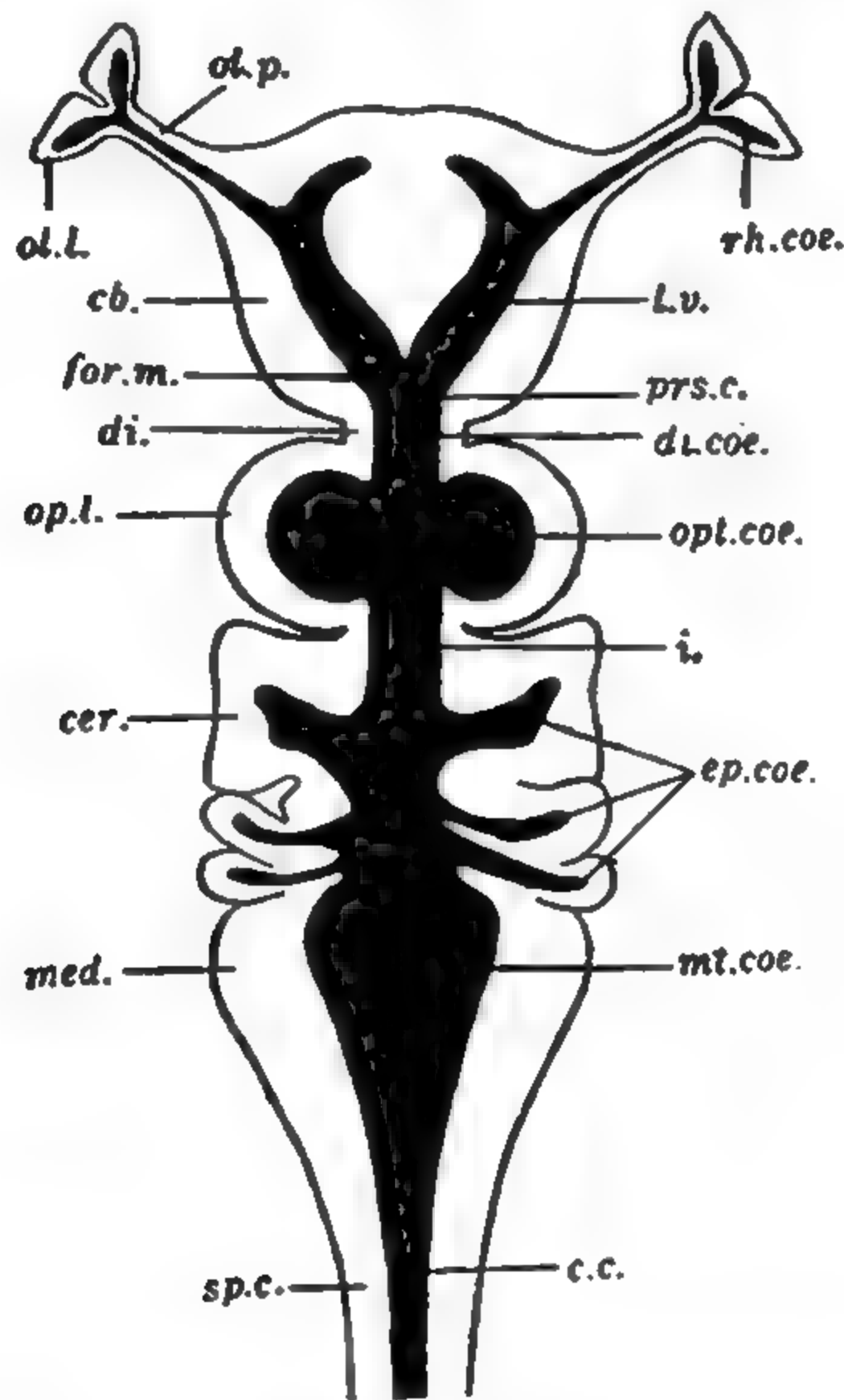


Fig. 72—A horizontal longitudinal section of the brain (semi-diagrammatic). *cb.*, cerebrum; *c.c.*, central canal; *cer.*, cerebellum; *di.*, diencephalon; *di. coe.*, diacoele; *ep. coe.*, epicoele; *for. m.*, foramen of Monro; *i.*, iter.; *l. v.*, lateral ventricle; *med.*, medulla oblongata; *mt. coe.*, metacoele; *o. l.*, olfactory lobe; *ol. p.*, olfactory peduncle; *op. l.*, optic lobe; *opt. coe.*, optocoele; *prs. c.*, prosocoele; *rh. coe.*, rhinocoele; *sp. c.*, spinal cord. (\times cir. $2\frac{1}{2}$).

tudinal bands, the *crura cerebri*. The third ventricle is a tubular chamber, the sides of which are thickened to form the optic thalami, the roof is thin and non-nervous and contains the *habenular ganglion* from which originates the *pineal stalk*, while the floor has an opening leading into the cavity of the infundibulum. The anterior wall of

the diencephalon remains very thin and is called the *lamina terminalis*, as it forms the actual anterior extremity of the embryonic fore-brain, the cerebral hemispheres being lateral outgrowths of the fore-brain which fuse together later to form the single globular cerebrum of the adult brain. The third ventricle continues in front into two long narrow cavities, the *lateral ventricles* of the cerebrum, which are separated from each other by a median partition, but communicate behind with the third ventricle through the *foramen of Monro*¹. The floor of the lateral ventricles is greatly thickened to form the bulging *corpora striata*. Each lateral ventricle communicates in front with the cavity of the olfactory lobe, the *rhinocoele*, through the tubular olfactory tract.

The *spinal cord* extends from the medulla oblongata almost to the end of the tail: in its external aspect it resembles that of the higher vertebrates, having a shallow *dorsal fissure* and a well-marked *ventral fissure*, but a transverse section through the cord shows that it consists of two halves connected together by a bridge which is traversed throughout its length by a narrow *central canal*. In the cord two regions can be distinguished: an outer region, the *white matter*,² composed of a non-nervous scaffolding formed by a network of spider-like *neuroglia cells* and the medullated nerve-fibres, and an internal region of *grey matter* containing chiefly the *neurones*.

(b) THE PERIPHERAL NERVOUS SYSTEM

The peripheral nervous system consists of the *cranial* and *spinal nerves* and the *autonomic nervous system*.

I. THE CRANIAL NERVES.

Ten pairs of nerves (fig. 73) arise from the brain, besides a pair of anterior terminal nerves.

The *first* or *olfactory nerve* arises as a number of fibres from each olfactory lobe, which are immediately distributed to the olfactory sac of its own side. The *terminal* or *pre-olfactory nerves* emerge from the ventral surface of the cerebrum through the neuro-

¹ This foramen is named in honour of three surgeons of this name who were father, son and grandson and made the unique record of holding the Chair of Anatomy at the University of Edinburgh for 126 consecutive years (1720-1846).

² The reason why the fibrous transmission part of the cord is "white" and the remaining inner part "grey" is that the sheaths on the medullated fibres of the neurones appear white, while the masses of cell-bodies without sheaths present a greyish appearance.

pore; each bears a ganglion (*ganglion terminale*) soon after its emergence (fig. 70) and runs at first beneath the cerebrum and then alongside the olfactory peduncle, to be distributed to the nasal septum and the external nostril.

The *second* or *optic nerve* arises from the optic thalamus. The nerve of each side crosses the other to form the *optic chiasma*, and passing over to the opposite side enters the orbit through the optic foramen and is distributed to the retina of the eye.

The *third* or *oculomotor* is a slender nerve arising from the ventral surface of the mid-brain; it enters the orbit through a small foramen lying slightly behind and below the aperture for the superficial ophthalmics of the fifth and seventh nerves; in the orbit it divides into branches, which supply the anterior, superior and inferior recti muscles and the inferior oblique muscle of the eye-ball (fig. 77).

The *fourth* or *trochlear nerve* arises from the dorso-lateral surface of the mid-brain, between the optic lobes and the cerebellum. It runs forward for a short distance within the cranial cavity and enters the orbit through a minute foramen in the upper border of the orbit, immediately above the optic foramen. It supplies the superior oblique muscle of the eye-ball.

The fifth, seventh and eighth nerves arise close together from the side of the medulla, immediately below the corpora restiformia.

The *fifth* or *trigeminal nerve* has originally three main branches: (i) the *ophthalmicus superficialis* (ii) the *maxillaris*, and (iii) the *mandibularis*. A fourth branch, the *ophthalmicus profundus* comes to be associated with the trigeminal nerve secondarily.

The *ophthalmicus superficialis* is a small branch which enters the orbit along with the *ophthalmicus superficialis* of the seventh nerve, and passes along the upper border of the orbit beneath the branch of the seventh; it then passes to the roof of the cranium through a notch in the anterior wall of the orbit. It is a purely sensory branch and supplies the skin of the snout in front of the olfactory capsules. The *ophthalmicus profundus* (fig. 73) arises from the anterior border of the root of the main nerve, runs forward a short distance within the cranial cavity and then enters the orbit through a small foramen close to and behind the foramen for the third nerve. In the orbit it passes forward between the dorsal and ventral branches of the third nerve, lying close to the wall of the cranium, above the optic nerve and the oblique muscles. It gives off a slender *ciliary nerve* to the eye-ball and passes forward to the anterior end of the

orbit, where it pierces the wall of the olfactory capsule and emerges again through an aperture on the roof of the olfactory capsule and breaks up into small branches supplying the skin of the dorsal surface of the snout.

The main branch of the fifth nerve comes out through the trigemino-facial foramen along with the main branch of the seventh nerve, and divides immediately into two branches, the *maxillaris* and the *mandibularis*. The *maxillaris* branch runs in two groups, the *maxillaris superior* and the *maxillaris inferior*. The *maxillaris superior* forms a flat ribbon-like nerve along the floor of the orbit, and runs close behind and almost parallel to the *buccalis* of the seventh nerve, lying ventrally to the eyeball and its muscles; it then travels outward and passes over the lower margin of the orbit and sends several branches to the skin of the upper jaw. The *maxillaris inferior* runs directly outward alongside the ramus mandibularis and innervates the posterior part of the upper lip. The *mandibularis branch* separates from the *maxillaris* soon after it enters the orbit and runs obliquely backward in the posterior angle of the orbit, lying dorsally to the palatine branch of the seventh nerve. It then passes over the upper surface of the palato-pterygo-quadratus, curves round the angle of the mouth and finally ends in small branches which innervate the muscles of the lower jaw. In the lower jaw the nerve lies immediately beneath the skin and runs along the hinder edge of the Meckel's cartilage.

The *sixth* or *abducens* is a slender nerve arising from the medulla oblongata close to the mid-ventral line; it enters the orbit through a foramen lying just behind that of the fifth and seventh nerves, and innervates the posterior rectus muscle of the eye-ball.

The *seventh* or *facial* is a large nerve which comes out of the cranium in two bundles: (i) the *ophthalmicus superficialis branch* which comes out of the cranium along with the similar branch of the fifth nerve, and consists of purely *acoustico-lateral elements* supplying the lateral line system¹ of receptor organs, (ii) a bundle of mixed sensory and motor fibres which comes out of the cranium along with the maxillary and mandibular branches of the fifth nerve and divides into: (a) a *ramus buccalis*, (b) a *ramus hyomandibularis*, and (c) a *ramus palatinus*. Of these three branches, the *buccalis* contains purely *acoustico-lateral elements*; the *hyomandibularis* also contains largely these very elements along with a few visceral sensory and visceral

¹ Kirtisinghe, P.—Notes on the course of the Lateral line Canals and the Cranial Nerves in the viviparous shark *Scoliodon*. Spolia Zeylanica, Vol. 17. 1932.

motor fibres, while the palatinus contains only visceral sensory fibres.

(i) The *ophthalmicus superficialis* is a large flattened nerve which enters the orbit by a large foramen in front of and above that of the *ophthalmicus profundus*, and extends along the upper border of the orbit close to the cranial wall, giving off several branches to the supra-orbital canal just above the eye. The main nerve, however, passes forward close to the pre-orbital process and reaches the dorsal surface of the snout where it divides into several branches supplying the entire length of the supra-orbital canal and all the ampullary organs in the region of the snout. It is a very large nerve and spreads over the entire dorsal surface of the snout right up to its tip (fig. 74).

(ii) The three branches of the bundle of mixed sensory and motor nerves are distributed as follows:

(a) The *ramus buccalis* (fig. 74) enters the orbit along with the maxillaris and mandibularis branches of the fifth and forms the great *buccalis-maxillo-mandibularis trunk*, but it soon separates from the mandibularis and runs across the floor of the orbit parallel to the superior maxillary of the fifth nerve. Soon after its emergence from the cranium, it gives off a few slender branches which supply the infra-orbital canal behind and below the eye. The main branch of the buccalis passes forward as a broad flattened nerve to the antero-ventral angle of the orbit, and near the orbital process of the palato-quadrate, turns downward and forward to the ventro-lateral side of the nasal capsule and passes to the ventral tip of the snout, giving off branches to the infra-orbital canal of the snout and its associated groups of ampullae.

(b) The *ramus hyomandibularis* runs backward and outward along the anterior face of the auditory capsule and comes to lie just beneath the skin of the cheek where it gives off a slender *optic branch* innervating the post-orbital canal and an *anterior branch* innervating the jugal canal. Both these branches are composed of acoustico-lateral fibres. The main hyomandibular nerve divides into *three* branches: (i) the mandibularis externus, (ii) the mandibularis internus, and (iii) the hyoidean. The *mandibularis externus* (fig. 74) is a slender nerve which passes backward and curves round the angle of the jaws and follows the course of the *mandibular canal* which it supplies. The *mandibularis internus* dips inward beneath the Meckel's cartilage and supplies visceral sensory fibres to the mucous membrane of the buccal floor. The *hyoidean branch* runs forward to supply visceral motor fibres to the muscles of the throat.

(c) The *ramus palatinus* (fig. 73, VII f), soon after its emergence from the cranium, runs across the floor of the orbit, and gives off small branches travelling outward to the roof of the pharynx, while the main branch travels along the edge of the floor of the orbit and innervates the roof of the buccal cavity. The palatinus branch is composed of visceral sensory fibres.

The *eighth or auditory nerve* arises close to the fifth and seventh, and divides immediately into two branches, the *vestibular* and the *saccular*, each of which divides again to supply the various parts of the membranous labyrinth of the internal ear (fig. 78). This nerve forms part of the acoustico-lateral system.

The *ninth or glosso-pharyngeal* arises from the ventro-lateral surface of the medulla, behind the origin of the sixth nerve, and runs obliquely backward within the floor of the auditory capsule; it emerges from the capsule through an opening in its posterior wall and immediately gives off a branch to the commissural occipital canal. It then passes backward and downward to the region of the first gill-cleft, where it divides into a small *pre-trematic branch* running along the anterior border of the gill-cleft, and a large *post-trematic branch* running along its posterior border. This nerve is mainly sensory and supplies the mucous membrane around the first gill-cleft and the pharynx, the post-trematic branch alone containing a few motor fibres supplying the muscles of the pharynx.

The *tenth or vagus* is the most widely distributed of all the cranial nerves. It arises behind the ninth from a number of roots and leaves the skull by a large foramen situated externally to the occipital condyle. It runs backward and gives off numerous branches, the chief of which are the *branchialis* supplying the gills, the *visceralis* supplying the internal viscera, and the *lateralis* supplying the lateral line receptor organs of the trunk.

The *branchialis* consists of four main nerves going around the second, third, fourth and fifth gill-clefts. Each nerve resembles the glosso-pharyngeal in its distribution, consisting of a pre-trematic and a pharyngeal branch. The first two nerves divide into these three branches immediately after they emerge from the cranial cavity, while the third and fourth run obliquely backward to the dorsal edges of their gill-clefts and there divide into their three branches. These branchial nerve-branches supply the mucous membrane around the gill-clefts and the pharynx, and also innervate the branchial muscles. The *visceralis* is a large nerve which runs backward into the body-cavity and innervates the internal

viscera, including the alimentary canal, liver, lungs and the heart. The *lateralis* arises dorsally to the other nerves and runs backward, parallel to the lateral line canal, in the deep fascia between the dorsal and ventral segments of the body-muscles. It gives off numerous small branches to the neuromast organs of the lateral line canal (fig. 74) all along its course. At its anterior end the *lateralis* gives off a *supra-temporal branch* to the commissural occipital canal.

The lateral line canals and the ampullary organs are supplied by several branches of the facial and the *lateralis* branch of the vagus. All these branches originate from a single centre in the medulla, the *tuberculum acousticum*, from which also originates the auditory nerve. In fact, the lateral line receptors and the receptors in the auditory labyrinth are genetically related to each other, the receptors of the labyrinth being merely specialized deeply sunk lateral line receptors.

The *occipito-spinals* (fig. 73) are one or two slender nerves which arise from the medulla close behind the roots of the vagus and emerge from the cranial cavity along with the vagus. They run backward closely along the *visceralis* branch and unite with the first six or seven spinal nerves forming a large trunk called the *cervical plexus*. This nerve-trunk runs backward and downward along the outer surface of the body-cavity right up to the anterior border of the pectoral fin, where it divides into three branches of unequal size; of these, the *posterior branch* or *brachial plexus* passes through a foramen in the pectoral girdle and supplies the muscles of the pectoral fin, the *mesial branch* is small and is distributed to the hypobranchial muscles, while the large *anterior branch* curves forward from the pectoral girdle and extends almost to the mid-ventral line of the pharynx, supplying branches to the pharyngeal muscles throughout its course.

II. THE SPINAL NERVES.

The *spinal nerves* (fig. 73) arise in pairs from the sides of the spinal cord. Each nerve arises by two roots, a *ventral* or *motor root* and a *dorsal* or *sensory root*. The ventral root always arises in front of the dorsal which bears a slight enlargement called the *ganglion of the dorsal root*. Both the roots run backward for a short distance within the neural canal, and perforate the cartilages of the neural arch separately, but unite outside to form a common mixed spinal nerve. Each spinal nerve divides into three branches: (i) *ramus dorsalis*, supplying the skin and muscles of the dorsal body-wall, (ii) *ramus ventralis*, supplying the skin and muscles of the ventral body-wall, and (iii) *ramus communicans* containing visceral sensory and motor fibres and joining the autonomic nervous system.

III. THE AUTONOMIC NERVOUS SYSTEM.

The *autonomic nervous system* consists of a paired series of irregularly arranged ganglia situated anteriorly in the dorsal wall of the posterior cardinal sinuses and posteriorly in the dorsal part of the kidney on each side of the mid-dorsal line. The first ganglion is small, but the second, called the *gastric ganglion*, is fairly large, being formed by the fusion of a number of ganglia; it is situated immediately behind the post-branchial plexus and is connected with numerous fibres from spinal nerves, and gives off branches to the viscera. The succeeding ganglia are small; there is always at least one ganglion in each segment, but often there are two or three in a segment. Sometimes the ganglia of successive segments are joined by longitudinal connectives, but there is no definite continuous chain such as occurs in Teleostei and Tetrapoda. The posterior ganglia innervate the genital ducts, kidneys, urinary sinus, the intestine and the rectum. The autonomic nervous system of fishes is not differentiated into functionally antagonistic sympathetic and parasympathetic systems, as it is in mammals.

FUNCTIONS OF THE NERVOUS SYSTEM

The nervous system co-ordinates and integrates all the activities and functions of the body in relation largely to the outer world. It receives all information of the changing environment through receptor organs and their sensory nerves and sends out orders through motor nerves to the muscles and glands (effector organs) for suitable action to meet the needs of the animal. The brain is an actively functioning organ with functions of learning and imitation and maintenance of drive; in fact, the central nervous system does not come to rest even when unstimulated. The brain of the shark is characterized by the great development of the cerebrum and cerebellum. In its search for food the shark depends mainly on its keen sense of smell and its cerebrum is largely a "smell brain". The cerebellum is the seat of regulation of balance and muscular control. A free active life in water demands a keen appreciation of balance combined with great muscular strength and agility of movements, and hence the great development of this control centre in the brain of the shark. The enormous development of the restiform bodies is ascribed to the development of the sensory centres of the lateral line nerves. The medulla contains the respiratory centres, besides others.

¹ Young, J.Z.—The Autonomic Nervous System of Selachians. Q.J.M.S., Vol. 75, 1932.

The autonomic nervous system looks after the involuntary work of the respiratory and circulatory organs and of the smooth muscles and the viscera. It is an independent sub-office, so to speak, which relieves the central nervous system of regulating the routine drudgery of living.

The neurons of the spinal cord are responsible for the rhythms of activity in locomotory muscles, but this activity is regulated by the hind-brain. When the spinal cord of a dogfish is transected behind the brain, some inhibiting influence from the brain is removed and the shark keeps swimming continuously without stopping until it dies ¹.

¹ Gray J.—Aspects of Animal Locomotion, *Proc. Roy. Soc., B.*, vol. 128, 1939.

CHAPTER X

THE RECEPTOR ORGANS

The receptor organs include the paired olfactory, optic and stato-acoustic organs as well as the characteristic receptor organs of fishes, *i.e.* the lateral line organs or neuromasts and the ampullae of Lorenzini.

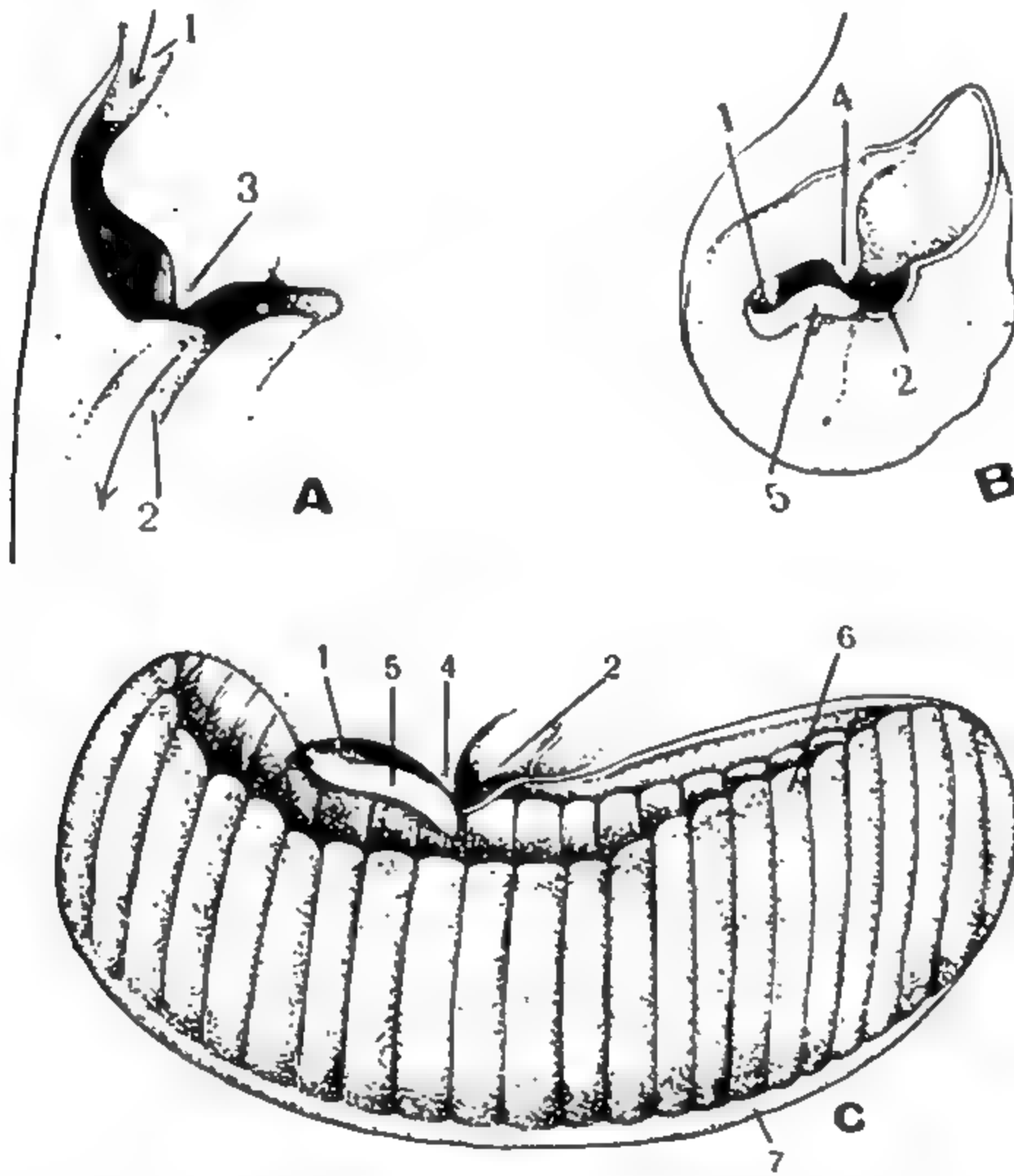


Fig. 75—A. A ventral view of the right naris. B. An inner view of the same. C. The olfactory sac dissected out to show its relation to the inner nasal flaps; 1, incurrent aperture; 2, excurrent aperture; 3, ventral nasal flap; 4 and 5, upper and lower inner nasal flaps; 6, Schneiderian folds; 7, median raphe.

THE OLFACTORY ORGANS (OLFACTORECEPTORS).

The olfactory organs are a pair of blind sacs situated on the ventral side of the head in front of the mouth. They are invagina-

tions of the ectoderm and retain their primitive openings to the exterior, but do not communicate with the buccal cavity by an internal opening. Each olfactory sac (fig. 75) is ellipsoid in shape and proportionately very large; it is covered externally by a thin membrane and is lodged on each side in the cartilaginous olfactory capsule (fig. 76); the mucous membrane lining its inner wall is thrown into a double series of folds, the *Schneiderian folds*, which are numerous and closely set and are held in place by a median band of connective tissue, the *median raphe*. The epithelium of the folds consists of *olfactory receptor cells* intermixed with stiff *supporting cells*. The olfactory cells are connected with the fibres of the olfactory nerve which passes from each olfactory sac to the olfactory lobe of its own side of the brain.

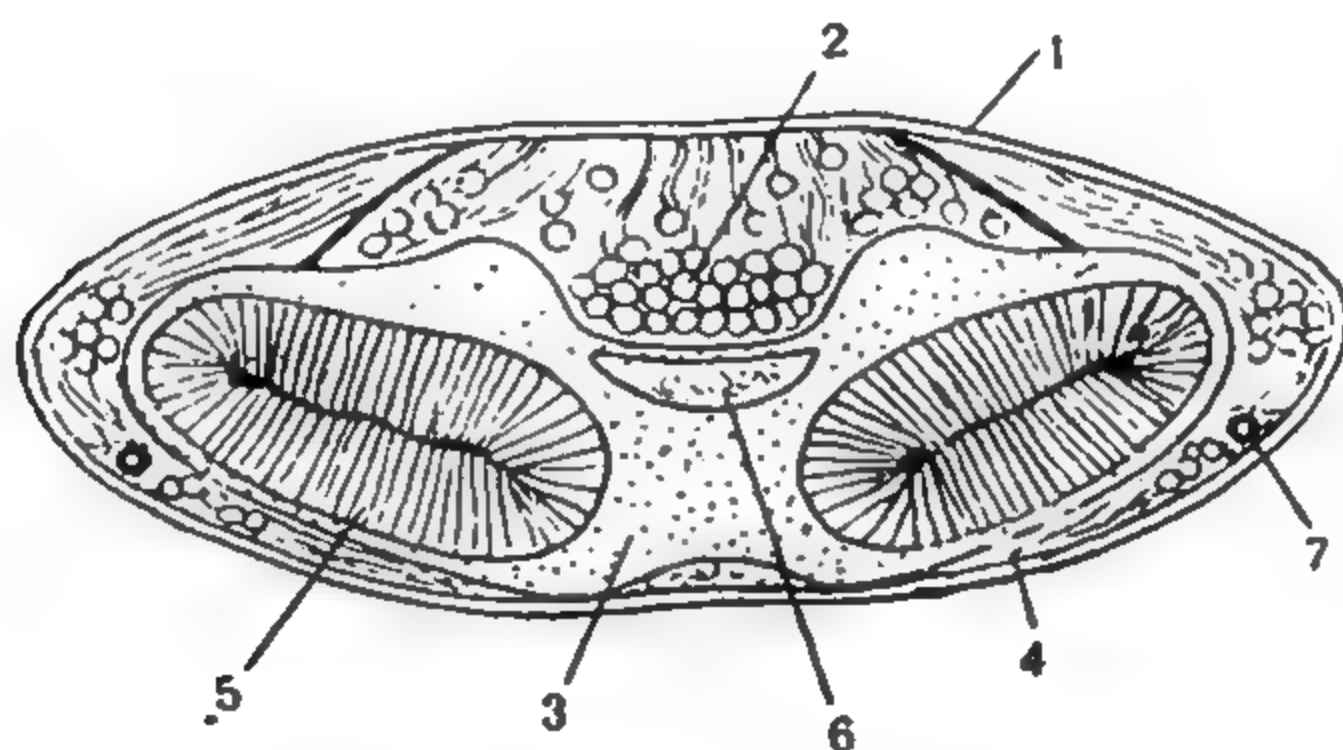


Fig. 76—A transverse section of the shark passing through the region of the olfactory sacs. 1, integument; 2, Lorenzini's ampullae; 3, ethmoidal cartilage; 4, cartilage of the olfactory capsule; 5, wall of the olfactory sac (Schneiderian folds); 6, muscles; 7, ventro-lateral branch of the supra-orbital canal. (\times cir. 2)

Each narial opening is functionally divided into two, a lateral *incurrent siphon* and a median *excurrent siphon* (fig. 82, A and B), by three nasal flaps, two of which project inwards fitting closely, one above the other, while the third hangs down from the dorsal side slightly overlapping the others. The median raphe of the Schneiderian folds lies parallel to the long axis of the nasal aperture, and therefore, the current of water which enters the incurrent siphon is at first directed against the oval wall of the olfactory sac, then turns internally to the nasal valve in the direction of the median raphe and finally passes out through the median excurrent siphon. The current, thus, takes a zig-zag course through the olfactory sac, entering at the lateral end of the nasal aperture and leaving it at its mesial end.

The great size of the olfactory sacs is characteristic of Elasmobranchs in general and is correlated with a highly developed sense of smell. Sheldon¹ demonstrated by a series of experiments, that of all the special receptors the olfactory receptors are probably of the greatest service to most Elasmobranchs. He found that when the external narial openings were plugged with cotton-wool so as to prevent any circulation of water through the olfactory sacs, the shark would swim over any food without detecting it by sight; on the other hand, if even one nostril was open, the shark was able to detect the food with great ease even though the food was concealed.

THE EYES (PHOTORECEPTORS).

Each eye is derived partly from an outgrowth of the fore-brain (optic vesicle) and partly from an ingrowth of the outer ectoderm together with the mesoderm. The eye-ball of the adult shark is formed of three concentric layers, the *sclerotic*, the *choroid* and the *retina*.

The *sclerotic* is cartilaginous and opaque and forms the outer protective layer of the eye. On the exposed surface of the eye, the sclerotic gives place to a large transparent membrane, the *cornea*, through which light enters. The sclerotic is lined internally by a connective tissue coat, the *choroid*, which is richly supplied with blood-vessels and is pigmented; it is continued in front as a strongly pigmented circular curtain, the *iris*, with a median vertical slit, the *pupil* (fig. 44), which cannot be enlarged or contracted in fishes. The *retina* is the innermost layer of the posterior region of the eye-ball and forms its percipient portion. It consists of elongated receptor cells, the *rods*, which are connected with fibres of the optic nerve spreading over the entire inner surface of the retina. The inner surface of the choroid is covered by a series of guanine plates forming the so-called *tapetum*, which serves to reflect back to the rods in the retina any incident light which has passed through them. Closely attached to the posterior surface of the iris lies the spherical *crystalline lens* which divides the eye into two unequal chambers, each filled with a semi-fluid substance. The chamber in front of the lens is filled with a saline liquid, the *aqueous humour*, while the chamber behind the lens contains a denser fluid, the *vitreous humour*. The lens is kept in place by a *suspensory ligament* which extends from the edge of the lens to the *ciliary processes* which are really a number of longitudinal folds of the choroid.

The eye-ball is lodged in the orbit and is held in position by six eye-muscles and a cartilaginous stalk, called the *optic pedicle*, arising

¹ Sheldon, R.E.—“The Sense of Smell in Selachians”, *Journal of Experimental Zoology*, vol. X, 1910.

from the posterior angle of the orbit. The eye-muscles are inserted on the eye-ball in two groups. The first group consists of four *recti* muscles which arise close together from the posterior angle of the orbit and are called the *superior rectus*, *inferior rectus*, *anterior rectus* and *posterior rectus* muscles. The *superior rectus* runs outward and upward to be inserted on the dorsal surface of the eye-ball; the *inferior rectus* runs outward and downward and is inserted on the ventral surface; the *anterior rectus* runs forward and outward and is inserted on the anterior surface; while the *posterior rectus* runs backward to be inserted on the posterior surface. The second group consists

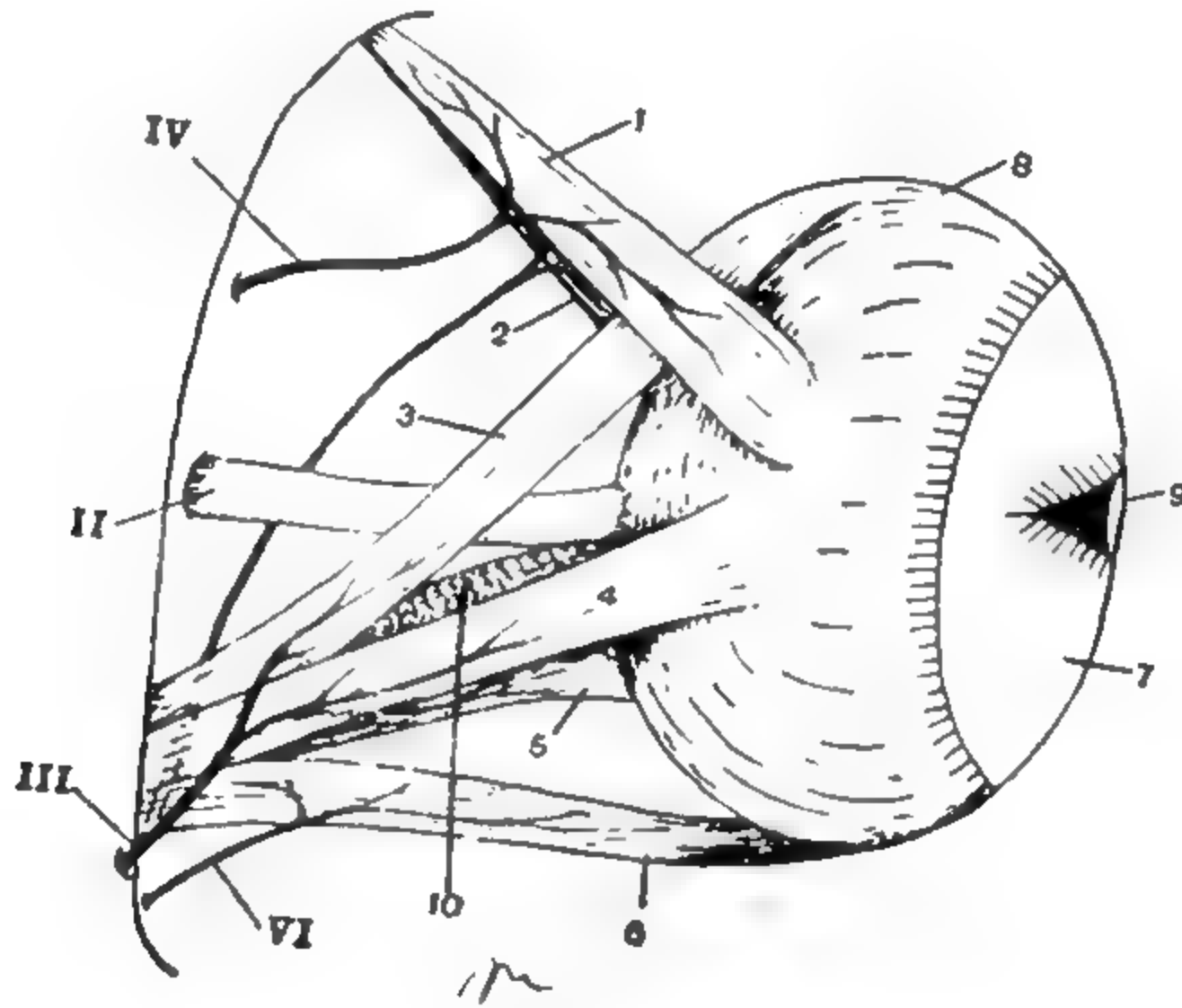


Fig. 77—The eye-muscles and their nerve supply. 1, superior oblique; 2, inferior oblique; 3, anterior rectus; 4, superior rectus; 5, inferior rectus; 6, posterior rectus; 7, cornea; 8, sclerotic coat; 9, pupil; 10, optic pedicle; II, optic nerve; III, oculo-motor nerve; IV, pathetic nerve; VI, abducens nerve.

of two *oblique* muscles which arise close together from the anterior angle of the orbit and run backward and outward to the eye-ball. The *superior oblique* is inserted on the dorsal surface of the eye-ball in front of the place of insertion of the superior rectus, while the *inferior oblique* is inserted on the ventral surface of the eye-ball in front of the inferior rectus.

The eyes of sharks are bigger in proportion to the rest of the body, but are so far separated from each other as to render it impossible for both of them to focus together on a given point. There is, therefore, no binocular vision and each eye has its own range of vision. Further, since little adjustment of the shape of the lens is

possible and the pupil is non-contractile, the power of estimation of distances is also poor. But the lens can project through the pupil against the rounded cornea, so that even rays of light entering at a very wide angle can be caught and focussed on the retina. A shark is normally long sighted, but as its retina is without cones, it is colour-blind.¹

THE STATO-ACOUSTIC ORGANS.

The *stato-acoustic organ*² (fig. 78) of each side is formed of a closed ectodermal sac, the *membranous labyrinth*, enclosed within its auditory capsule. It consists of a central part, the *otosaccus*, and three peripheral *semi-circular canals*, orientated at right angles to one another in the three planes of space. The otosaccus is laterally compressed and is differentiated into a dorsal and anterior part, the *utricle*, and a ventral and posterior part, the *sacculus*. Each semi-circular canal is dilated at one end into a bulbous *ampulla* but opens at both ends into the otosaccus. From the top of the utricle arise the *anterior vertical* and *horizontal semi-circular canals*; their ampullae lie close together and open anteriorly into the middle of the utricle. Beneath these ampullae the utricle gives off an anterior outgrowth, the *recessus utriculi*. The sacculus gives origin dorsally to the *posterior vertical semi-circular canal* which forms a complete circle and opens posteriorly by its ampulla back into the *lagena cochleae* which is only a posterior outgrowth of the sacculus. The labyrinth of the Selachians is distinguished by a marked independence of the semi-circular canals from the otosaccus.

The whole of the labyrinth, including the semi-circular canals, is filled with a fluid, the *endolymph*, containing in addition one or more calcareous bodies, the *otoliths*. The cavity of the sacculus communicates with the exterior through a long tube, the *ductus endolymphaticus*, which runs upward and pierces the roof of the cranium within the parietal fossa (fig. 47) to open to the exterior by a minute pore in front of the commissural occipital canal (fig. 79). The space between the membranous labyrinth and the wall of the auditory capsule is filled with a fluid called the *perilymph*. The perilymphatic space opens to the exterior by a large aperture, the *fenestra*, situated immediately behind the opening of the *ductus endolymphaticus* (fig. 47).

The membranous labyrinth is innervated by the auditory nerve which divides into two branches: the anterior branch supplies

¹ Pincher, Chapman,—Vision in Fishes, *Discovery*, July, 1947.

² Shyam Sunder Lal—The internal ear of *Scoliodon sorrakowah*. *Proc. Ind. Acad. Sci.*, Vol. IX, 1939.

the recessus utriculi and the ampullae of the anterior and horizontal semi-circular canals, while the posterior branch supplies the sacculus, lagena and the ampulla of the posterior semi-circular canal. In each of the various divisions of the otosaccus as well as in the ampullae of the semi-circular canals, there are groups of delicate receptor cells bearing stiff hairs (*maculae*).

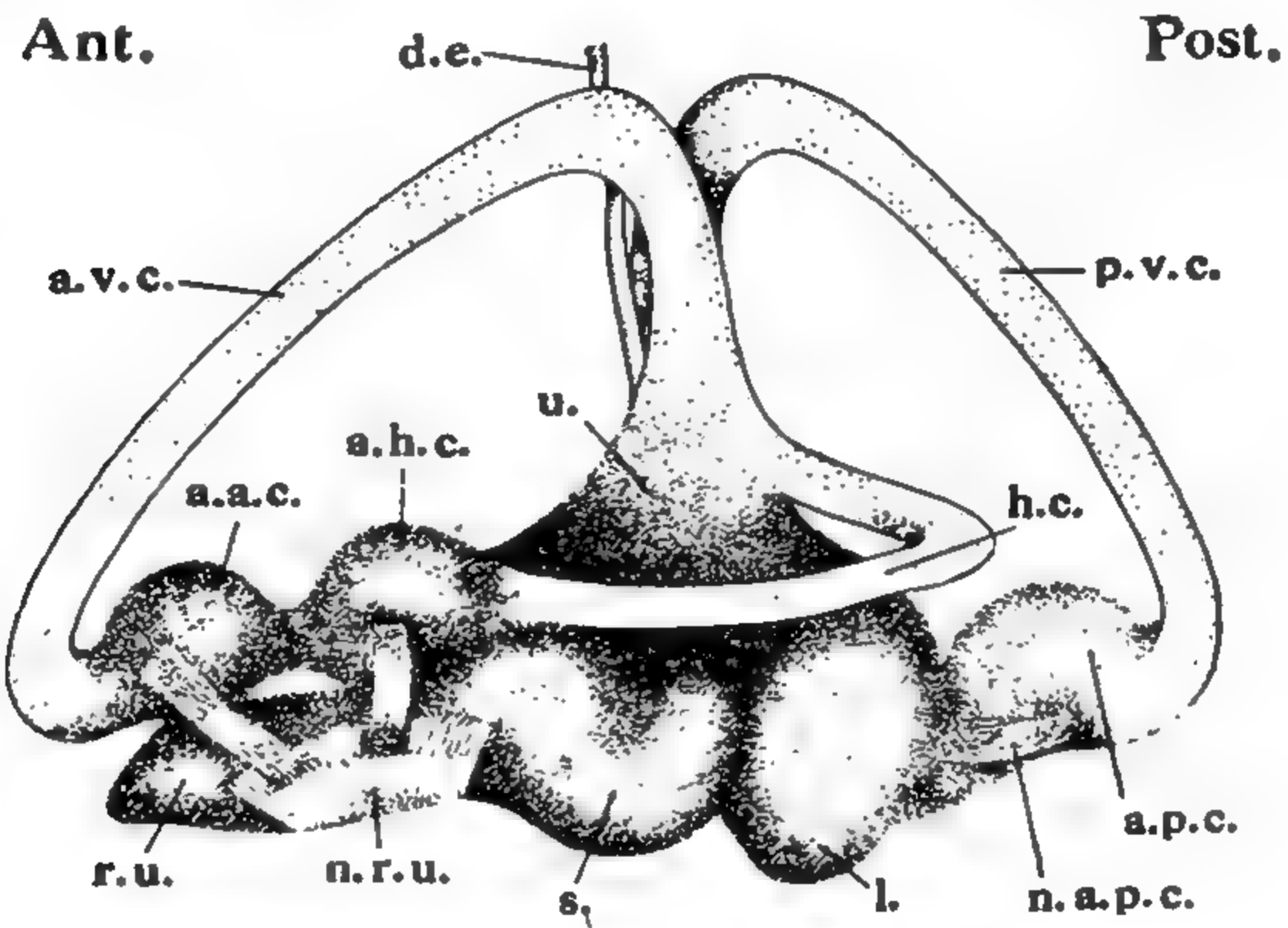


Fig. 78—An outer view of the left membranous labyrinth. *a.a.c.*, ampulla of the anterior vertical canal; *a.h.c.*, ampulla of the horizontal canal; *a.p.c.*, ampulla of the posterior vertical canal; *a.v.c.*, anterior vertical canal; *d.e.*, ductus endolymphaticus; *h.c.*, horizontal canal; *l.*, lagena cochleae; *n.a.p.c.*, nerve supplying the ampulla of the posterior vertical canal; *n.r.u.*, nerves supplying the recessus utriculi and the ampullae of the anterior vertical and horizontal canals; *p.v.c.*, posterior vertical canal; *r.u.*, recessus utriculi; *s.*, sacculus; *u.*, utriculus. (\times cir. 6). Modified from S. S. Lal.

The membranous labyrinth and its contained receptor organs have two distinct functions. The utricle and the semi-circular canals with their ampullary receptors are concerned exclusively with the non-acoustic function of the maintenance of balance or static and dynamic equilibrium (*statoreceptors*), movements of the fluid in any or all of the semi-circular canals being appreciated by their appropriate receptors¹. The saccule and its lagena together, on the other hand, receive auditory stimuli and form the organ of hearing (*acoustic receptors*).

¹ Lowenstein, Otto—Oscillographic analysis of the non-acoustic functions of the vertebrate ear. *Nature*, April 24, 1948.

THE NEUROMAST ORGANS (RHEORECEPTORS).

The *neuromast organs* consist of: (1) lateral line receptors and (2) pit-organs. The lateral line receptors lie in the *lateral line canal* on each side of the trunk and tail, each of which is continued into the *cephalic canals* on the head. These canals lie in the dermis and have groups of epidermal receptors or *neuromasts* imbedded in their walls, the neuromasts being innervated by the branches of the seventh nerve and the lateralis branch of the vagus. Small tubes emerge from these canals and open on the surface through minute pores.

Each *lateral line canal* (figs. 60, 61 and 66) lies within the skin at the junction of the dorsal and ventral divisions of the lateral muscles and extends from the tip of the tail to the back of the head (fig. 43). On reaching the head each canal bends dorsally and is connected with its fellow of the opposite side by a transverse commissure known as the *commissural occipital canal* (fig. 79), lying immediately behind the openings of the endolymphatic ducts. In front of the commissural canal, each lateral line canal or the cephalic canal, as it is now called, bends a little outward and forms the *post-orbital canal* which runs up to the posterior margin of the orbit, where it divides into two canals, the *supra-orbital* and the *infra-orbital*.

The *supra-orbital* (fig. 79, *so.c.*) runs close to the upper border of the orbit, but soon divides into two branches: of these, the *dorsal branch* (*d.br.*) loops towards the mid-dorsal line and runs up to the tip of the snout where it bends sharply backward and continues along the ventro-lateral edge of the snout as the *ventro-lateral branch* to a little distance behind the naris; the other branch, called the *anterior branch* (*a.br.*), bends downward just in front of the eye and joins the infra-orbital canal. The *infra-orbital* divides from the supra-orbital just behind the eye and bends sharply downward to run along the ventral margin of the orbit to the anterior angle of the eye, where it meets the anterior branch of the supra-orbital. It now curves ventrally and joins the ventro-lateral branch of the supra-orbital, and then runs transversely inward to join its fellow of the opposite side in front of the palato-quadrate symphysis (fig. 80). The fused infra-orbitals run forward a short distance in the mid-ventral line but separate again and run almost parallel to each other to the tip of the snout to join the supra-orbital canal there.

At the junction of the infra-orbital with the ventro-lateral branch of the supra-orbital arises the *jugal canal* just in front of the eye, which runs backward parallel to and beneath the infra-orbital canal, almost to the first gill-cleft. A short branch from the infra-orbital joins the

jugal canal behind the orbit. At the angle of the jaws, the jugal canal gives off the *mandibular canal* which runs along the lower jaw right up to its tip.

In some Elasmobranchs and in *Chimaera*, the lateral line system has the form of an open groove throughout life. This fact taken together with the development of the system indicates that the lateral line has originated from a groove of the skin which has closed and has become imbedded in the dermis or in the sub-cutaneous tissue.

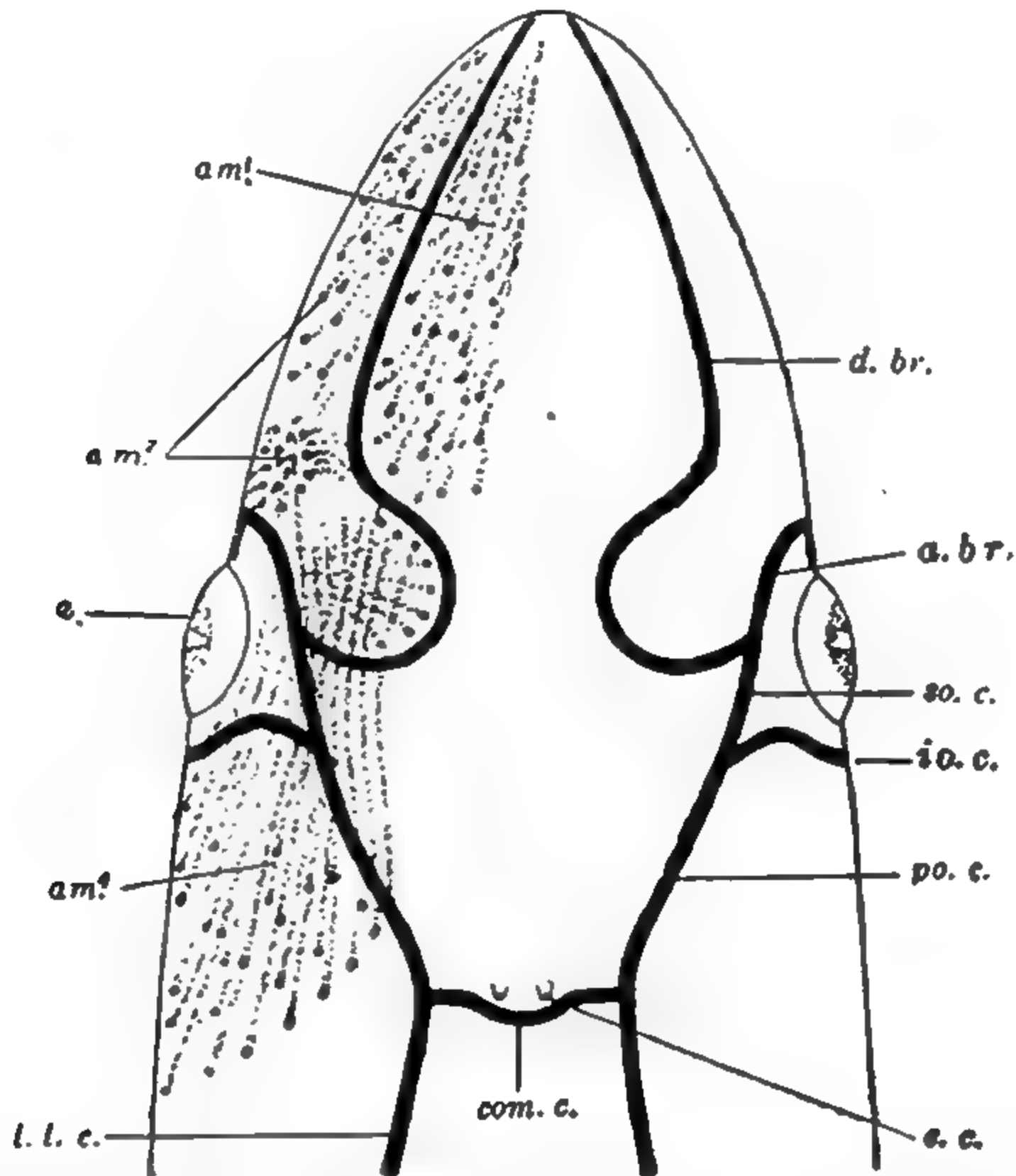


Fig. 79—A dissection of the dorsal surface of the head of *Scoliodon serrakowah*, showing the course of the lateral-line and cephalic canals, and the distribution of Lorenzini's ampullae (shown on the left side only). *a.br.*, anterior branch of the supra-orbital canal; *am1.*, supra-ophthalmic ampullae; *am2.*, outer buccal ampullae; *am4.*, posterior group of supra-ophthalmic ampullae; *com. c.*, commissural occipital canal; *d.br.*, dorsal branch of the supra-orbital canal; *e.*, eye; *e.c.*, external opening of ductus endolymphaticus; *io.c.*, infra-orbital canal; *l.l.c.*, lateral-line canal; *po.c.*, post-orbital canal; *so.c.*, supra-orbital canal. (about natural size).

THE PIT-ORGANS.

The *pit organs* are independent receptor organs sunk in pits which occur on the dorsal and lateral surfaces of the head (fig. 81).

They consist of ectodermal pits beneath which lie groups of receptor cells innervated by the nerve-fibres. The pit-organs are specially abundant in rays.

Parker¹ has shown that the receptors of the lateral line system are stimulated by slow vibrations of the watery environment and serve

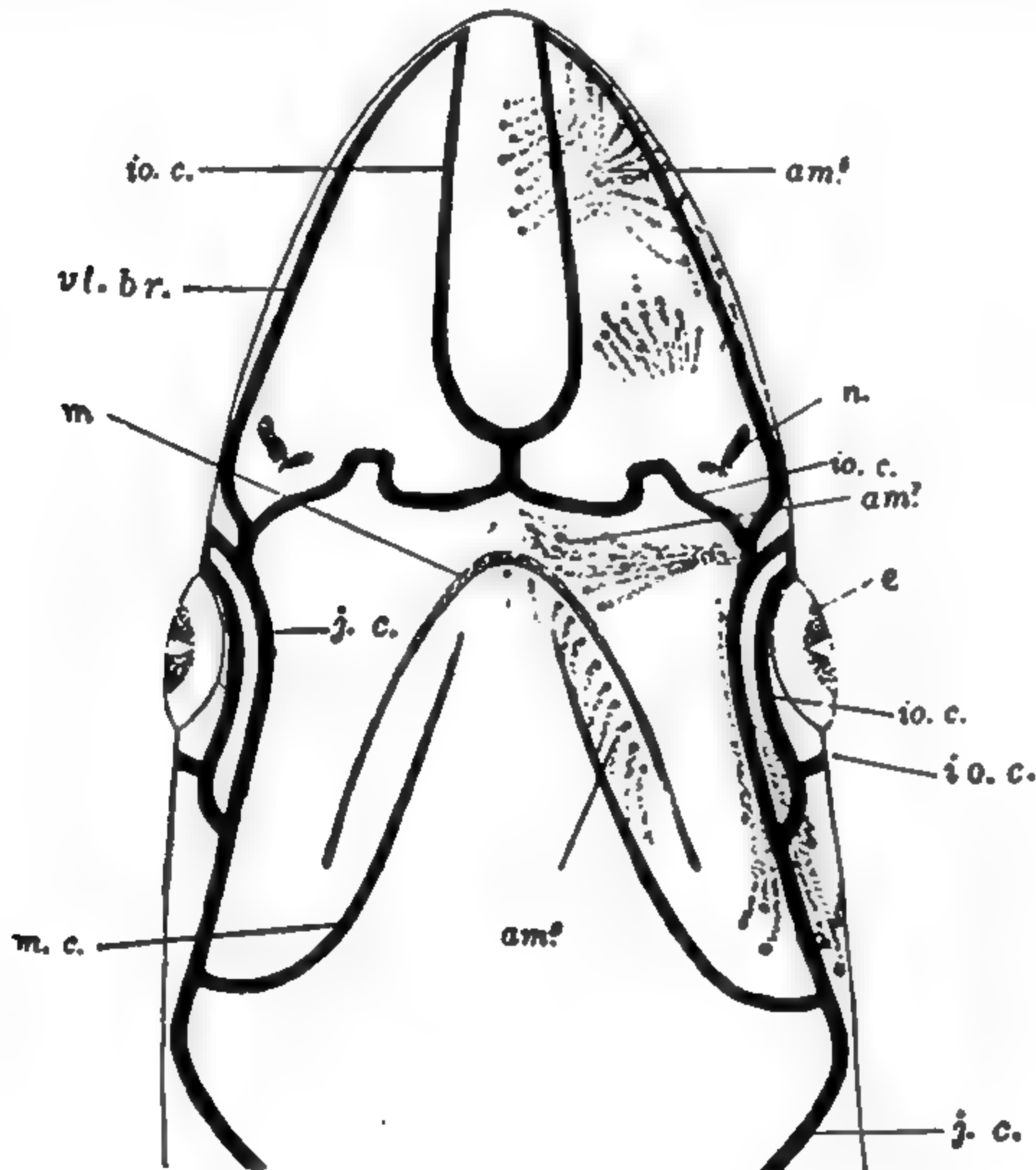


Fig. 80—A dissection of the ventral surface of the head, showing the course of the cephalic canals and the distribution of Lorenzini's ampullae (shown on the left side only). *am6.*, inner anterior group of buccal ampullae; *am7*, posterior group of inner buccal ampullae; *am9.*, mandibular ampullae; *e.*, eye; *io.c.*, infra-orbital canal; *j.c.*, jugal canal; *m.*, mouth; *m.c.*, mandibular canal; *n.*, nostril; *vl.br.*, ventro-lateral branch of the supra-orbital canal. (about natural size)

for the orientation of the body in relation to waves and currents: they are therefore termed *rheoreceptors* or current receptors. He found that a shark deprived of sight and hearing responded to wave-movement produced by throwing a stone into the water, but when

¹ Parker, G.H.—"Functions of the Lateral Line Organs," Bull. Bur. Fish., Vol. 24, 1904.

the lateral line nerves were cut, there was no response to these vibrations. The lateral line system, therefore, enables a fish to detect even the slightest disturbance in the surrounding medium in the comparative or complete darkness of deep water. Sand¹ has demonstrated that mechanical stimulation of the lateral line as well

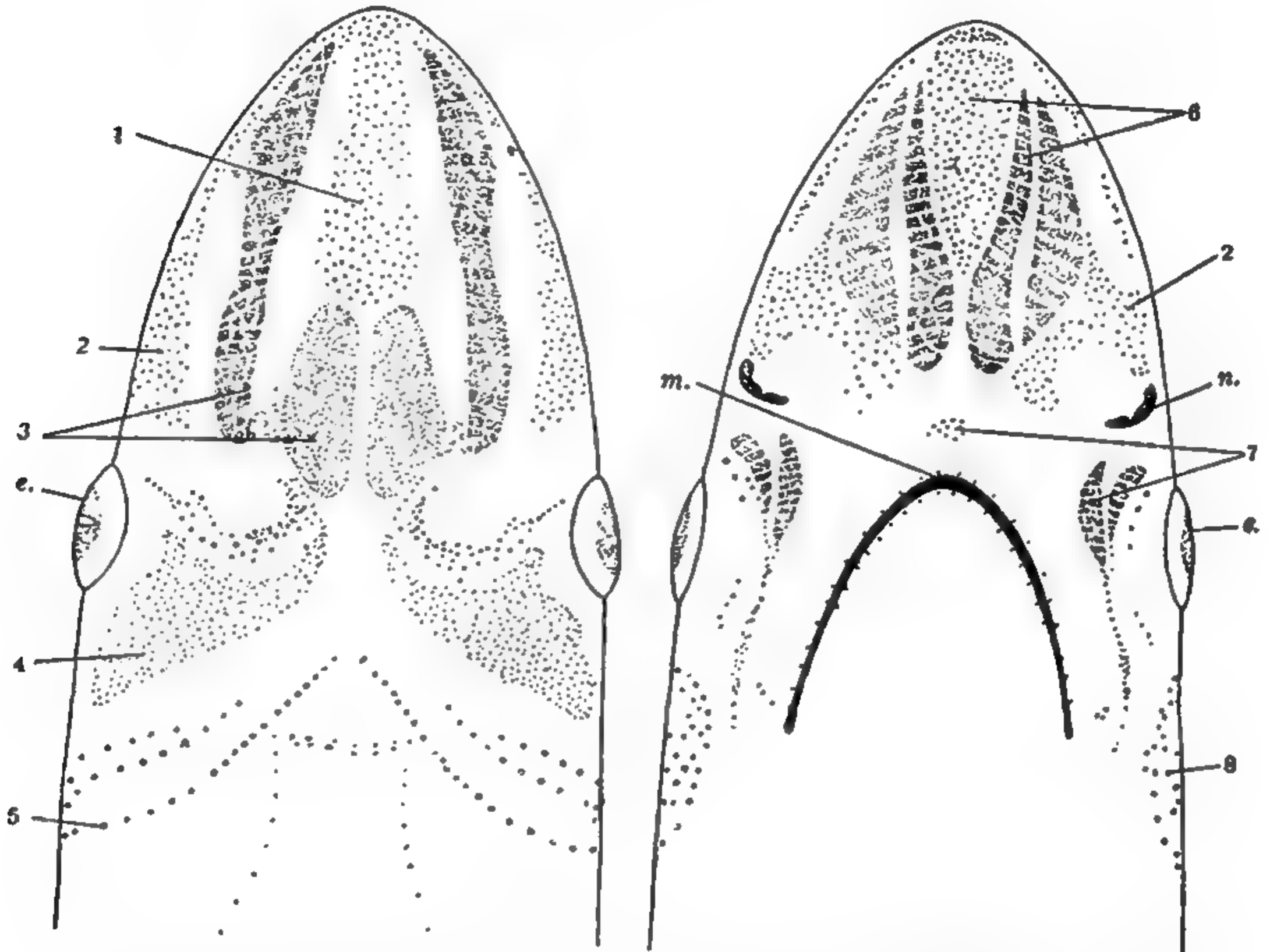


Fig. 81.—The ampullary pores on the head of *Scoliodon sorrakowah*. A, dorsal view; B, ventral view. 1, pores of the anterior group of supra-ophthalmic ampullae; 2, pores of the outer buccal ampullae; 3, pores of the middle group of the supra-ophthalmic ampullae; 4, pores of the posterior group of the same; 5, pit-organs; 6, pores of the inner anterior group of buccal ampullae; 7, pores of the posterior group of inner buccal ampullae; 8, pit-organs; e., eye; m., mouth; n., nasal aperture. (about natural size)

as vibrations propagated from a distance are effective in exciting the receptors on account of the movements they cause to occur in the endolymph of the lateral line canals. The flow of the endolymph in one direction is excitatory, but in the opposite direction it is inhibitory.

¹ Sand, A.—“Mechanism of the Lateral Sense Organs of fishes.” *Proc. Roy. Soc.*, Vol. 123, 1937.

THE AMPULLAE OF LORENZINI (THERMORECEPTORS)

On the dorsal and ventral surfaces of the head, hundreds of pores open to the exterior (figs. 79, 80 and 81); each of these pores leads into an elongated tube which ends in a radially septate ampullary sac lying deeply beneath the skin and free from it; each ampullary sac (fig. 82) consists of eight to nine radially dilated chambers arranged around a central core, the *centrum*. The ampullae lie together in clusters looking like bunches of grapes. Two kinds of cells are found in the ampullae: *pear-shaped gland cells* which secrete the jelly filling the the ampullary tubules, and the *pyramidal cells* with sense-

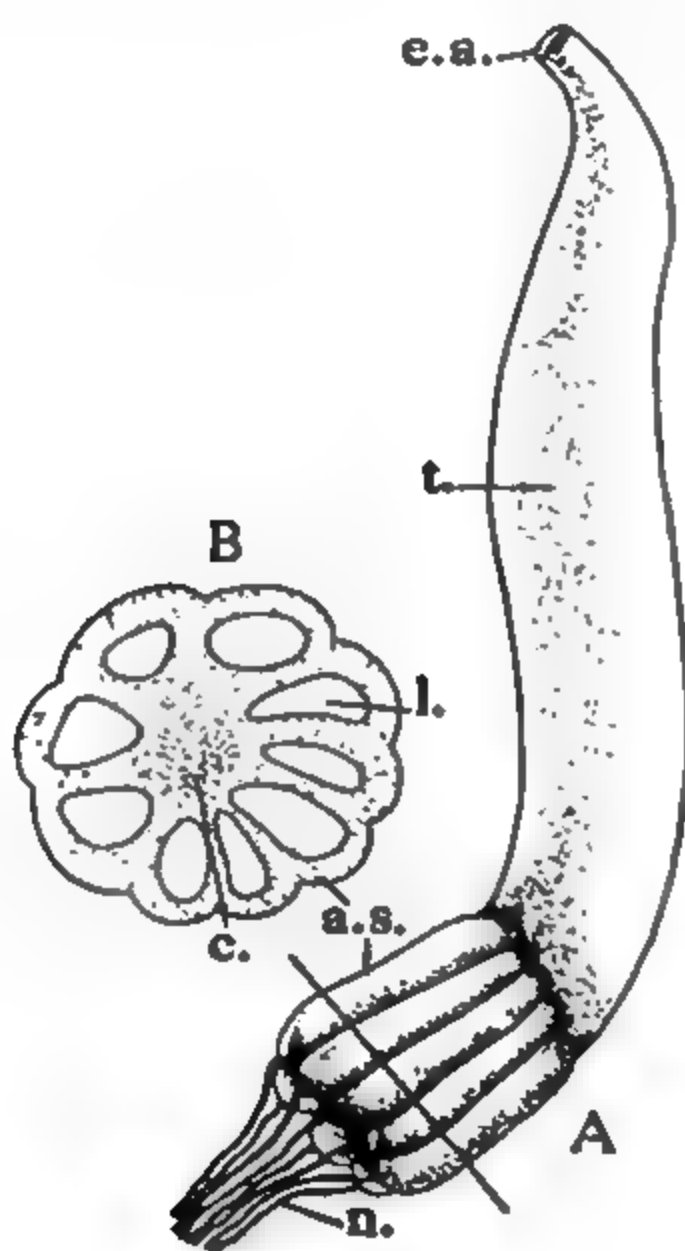


Fig. 82—A. An ampulla of Lorenzini, B. A section through an ampullary sac. a.s., ampullary sacs; c., centrum; e.a., external aperture; l., lumen of one of the radial dilatations of the ampullary sac; n., nerve-branches; t., tubule.

hairs forming the receptor cells. All the groups of ampullae are innervated by the superficial ophthalmic, buccal and hyomandibular branches of the facial nerve.

The ampullae are named according to their location in the head: the *supra-ophthalmic* group lies around the supra-orbital canal, the *outer buccal* between the supra-orbital and infra-orbital canals, and the *inner buccal* beneath the infra-orbital canal (fig. 79, 80 and 81).

The ampullae of Lorenzini were formerly regarded as neuro-mast organs of the same kind as the lateral line receptors and pit-organs. But Sand¹ has recently proved that these ampullae have no mechanical sensitivity whatever, but are really temperature receptors of sharks and rays. They have a rhythmic nervous activity, sending impulses to the brain at a steady rate. When the temperature of water rises between a range of 3° to 23°C, this rate decreases, but when the temperature falls below 3°C the rate increases. The brain is thus made aware of changes of temperature in the water by means of these ampullary receptors. Once the brain has noted the change of temperature, the steady impulse rate is resumed until a further change occurs. By this mechanism a skate responds to changes in water temperature of less than $\frac{1}{9}$ °C.

¹ Sand, A.—The Functions of the Ampullae of Lorenzini, *Proc. Roy. Soc.* Vol. 125, 1938.

CHAPTER XI

THE URINOGENITAL SYSTEM

In Vertebrates the excretory system develops as a series of paired glandular tubules with or without a ciliated funnel opening into the coelom. These kidney-tubules arise typically in three sets, developing in succession from in front backwards. The first set arises far forward in the coelom, close behind or within the pericardial cavity and constitutes the *pronephros*. In the shark the pronephric tubules are never functional and disappear altogether in the adult, but they open on each side into a longitudinal duct, the so-called *pronephric duct*, which persists in the adult even after the disappearance of the pronephric tubules, and runs behind to open into the cloaca. The next set of tubules which develop behind the pronephros are known as the *mesonephros*. A typical mesonephric tubule consists of: (i) a ciliated *peritoneal funnel* by means of which the tubule communicates with the coelom, (ii) a Bowman's capsule with a vascular tuft, the *glomerulus*, which acts as a filter for the blood-plasma and its waste contents and (iii) a coiled absorbing and conducting tubule. These tubules open into the persistent longitudinal duct, which is now called the *mesonephric duct*. In the lower Craniata the mesonephros forms the functional kidney of the adult and the mesonephric duct forms the ureter in the female and the urinogenital duct in the male. In higher vertebrates a third set of tubules, called the *metanephros*, arise behind the mesonephros and form the functional kidney of the adult.

In *Scoliodon* and other Elasmobranchs the *mesonephros* forms the adult kidney, but there is a marked tendency towards a differentiation of its posterior part so that the kidney is reduced in front but greatly developed behind: such a type of kidney has been called the *opisthonephros*¹, a term suggested by Graham Kerr to include "the whole series of tubules behind the pronephros in the lower Gnathostomes where a true metanephros is not present." Most of the peritoneal funnels are usually closed in the adult and the mesonephric duct splits longitudinally into two tubes, a dorsal and a ventral. The dorsal is called the *Wolffian duct* and forms the *vas deferens* of the

¹ Graham Kerr, J.—Text-Book of Embryology, Vol. II, London, 1919.

male, connected anteriorly with the *vasa efferentia* from the testis; the ventral tube is the *Mullerian* duct which forms the oviduct and the uterus in the female, but is abortive in the male. The mesonephric tubules of the functional opisthonephros open directly either into the cloaca or into the posterior section of the Wolffian duct.

(a) THE MALE URINOGENITAL ORGANS.

The kidneys (fig. 83) are a pair of long ribbon-like glandular structures lying dorsally to the peritoneum and extending from the root of the liver in front to the side of the cloaca behind. The posterior region of the kidney is greatly thickened and laterally compressed, and forms the chief organs of excretion, while the anterior region is reduced and becomes comparatively narrow and takes on the function of conveying genital products, and is therefore called the *epididymis* or the *organ of Leydig*. The substance of the kidney is made up of coiled glandular tubules, each of which consists of a *peritoneal funnel*, a *Bowman's capsule* enclosing the *glomerulus* and a coiled *renal tubule*, several of which open into a *common collecting tubule*. The renal tubules of elasmobranchs are peculiar in having developed a special urea-absorbing segment in them; its function is to reabsorb urea from the glomerular filtrate as it passes down the renal tubules (cf. p. 69). The collecting tubules of the anterior region of the kidney are exceedingly small and open into the *Wolffian duct*, while in the posterior region the collecting tubules open independently into a common duct, the *ureter*, which finally opens into a wide chamber, the *urinogenital sinus* (fig. 83). The urine is hypotonic to blood (Pp. 68-69 and 110).

The *testes* are a pair of elongated structures made up of numerous lobules with a median central canal; they are situated in the roof of the abdominal cavity and extend from the base of the liver in front to the caecal gland behind, being attached to the dorsal body-wall by folds of peritoneum called the *mesorchia*, and to the caecal gland behind by a non-glandular tissue. The spermatozoa from the testes pass through minute tubules, the *vasa efferentia*, into the anterior end of the Wolffian duct, now called the *vas deferens*, which

Fig. 83—The male urinogenital organs. 1, septum transversum; 2, anterior end of the kidney; 3, testis; 4, liver; 5, oesophagus; 6, vasa efferentia; 7, Wolffian duct (vas deferens); 8, posterior part of the kidney (opisthonephros); 9, vesicula seminalis; 10, sperm-sac, 10a, opening of sperm-sac; 11, ureter; 11a, opening of the ureter; 12, urinogenital sinus; 12a, urinogenital papilla; 13, rectum; 13a, opening of the rectum; 14, abdominal pore; 15, pelvic fin; 16, clasper; 17 upper, caecal gland; 17 lower, cloaca.

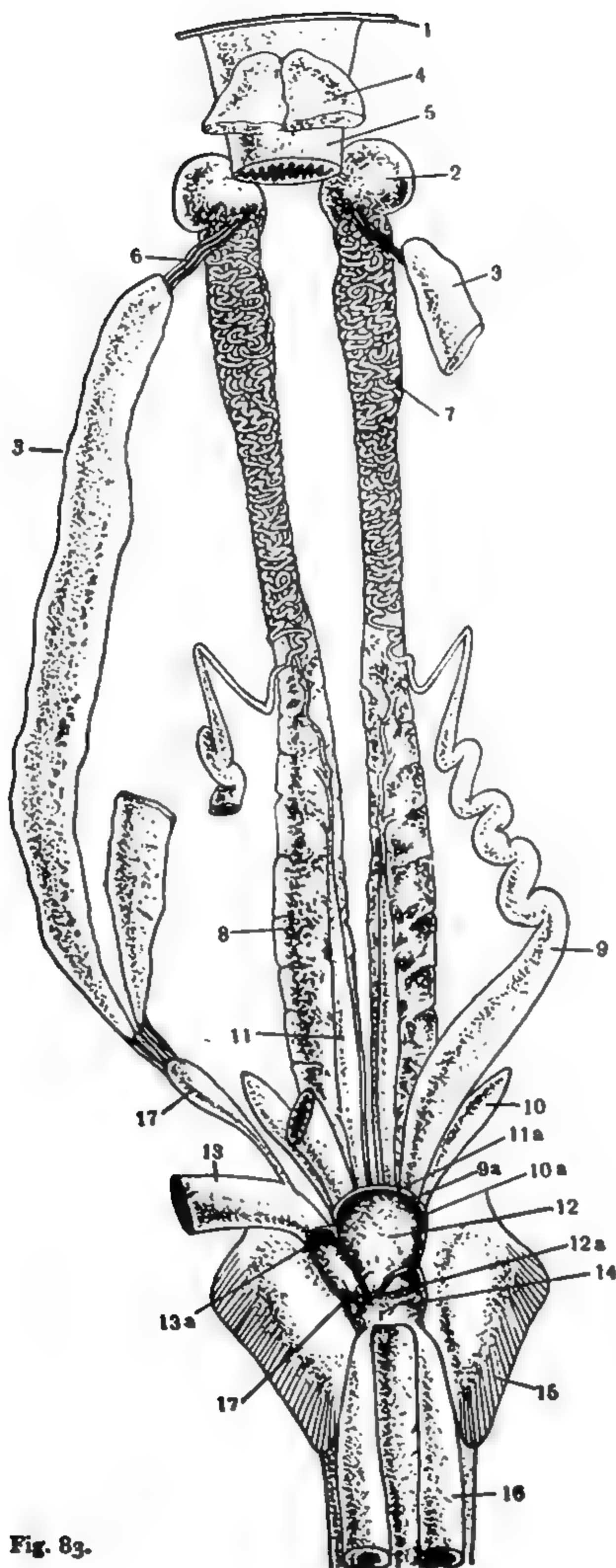


Fig. 83.

forms a narrow closely coiled tube occupying the greater part of the anterior section of the kidney. but becomes very much enlarged behind to form the *vesicula seminalis* (figs. 83 and 84). In the breeding season myriads of spermatozoa are found adhering to the walls of the *vesiculae seminales*. The *vesiculae seminales* of the two sides open behind into a large triangular chamber, the *urinogenital sinus*, which in its turn opens into the cloaca on an elevated *urinogenital papilla*. On either side of the *urinogenital sinus* lies a club-shaped *sperm-sac* which is really an outgrowth of the *urinogenital sinus*. During copulation the sperms pass into the claspers which are inserted into the cloaca of the female (P. 104).

There is a pair of elongated glandular sacs, the *siphons*, lying just beneath the skin of the ventral surface of the body of the male shark. These sacs extend anteriorly almost to the level of the posterior margin of the pectoral fins where they end blindly. Posteriorly, however, these sacs are continued as *siphon-tubes*, each of which opens into the proximal portion of the groove of the clasper of its own side (fig. 54, o.s.). The *siphons* have muscular and glandular walls but have no direct communication with the male *urinogenital* organs except that they open into the groove of the clasper. Leigh Sharpe¹ made a series of experiments and observations on the contents of the *siphons* and showed that these sacs never contained sperms but were usually full of sea-water. It is believed that the function of the sacs is to force the sperms from the cloaca into the clasper-grooves by a current produced by the sea water contained in these sacs.

(b) THE FEMALE URINOGENITAL ORGANS.

The female organs differ from those of the male in that there is no direct connection between the kidneys and the genital organs and that the anterior part of each kidney is extremely reduced. Consequently the anterior region extending as far forward as the base of the liver forms a long narrow strand, while the posterior region of the kidney is thick and massive, as in the male and extends to the posterior limit of the cloaca. The ureters are a pair of long thin-walled tubes that receive collecting tubules all along their length; they differ from those of the male in that the two ureters unite and open behind by a single median *urinary aperture* into the triangular chamber, here called the *urinary sinus*, since only excretory products from the kidneys are emptied into it. The *urinary papilla*

¹ Leigh Sharpe, W.H.—The Comparative Morphology of the secondary sexual characters of Elasmobranch Fishes. Memoirs I and II, Journal of Morphology. Vols. XXXV and XXXVI, 1920.

is similar to that of the male and bears a pore through which the urinary sinus opens into the cloaca.

The paired *ovaries*, varying in form and size according to the age of the shark, are situated one on either side of the vertebral column, just behind the base of the liver, where they are suspended on each side by a fold of peritoneum, the *mesovarium*. Between the ovary in front and the caecal gland behind extends a long tubular strand of tissue, the *epigonal organ* (fig. 85). In the breeding season

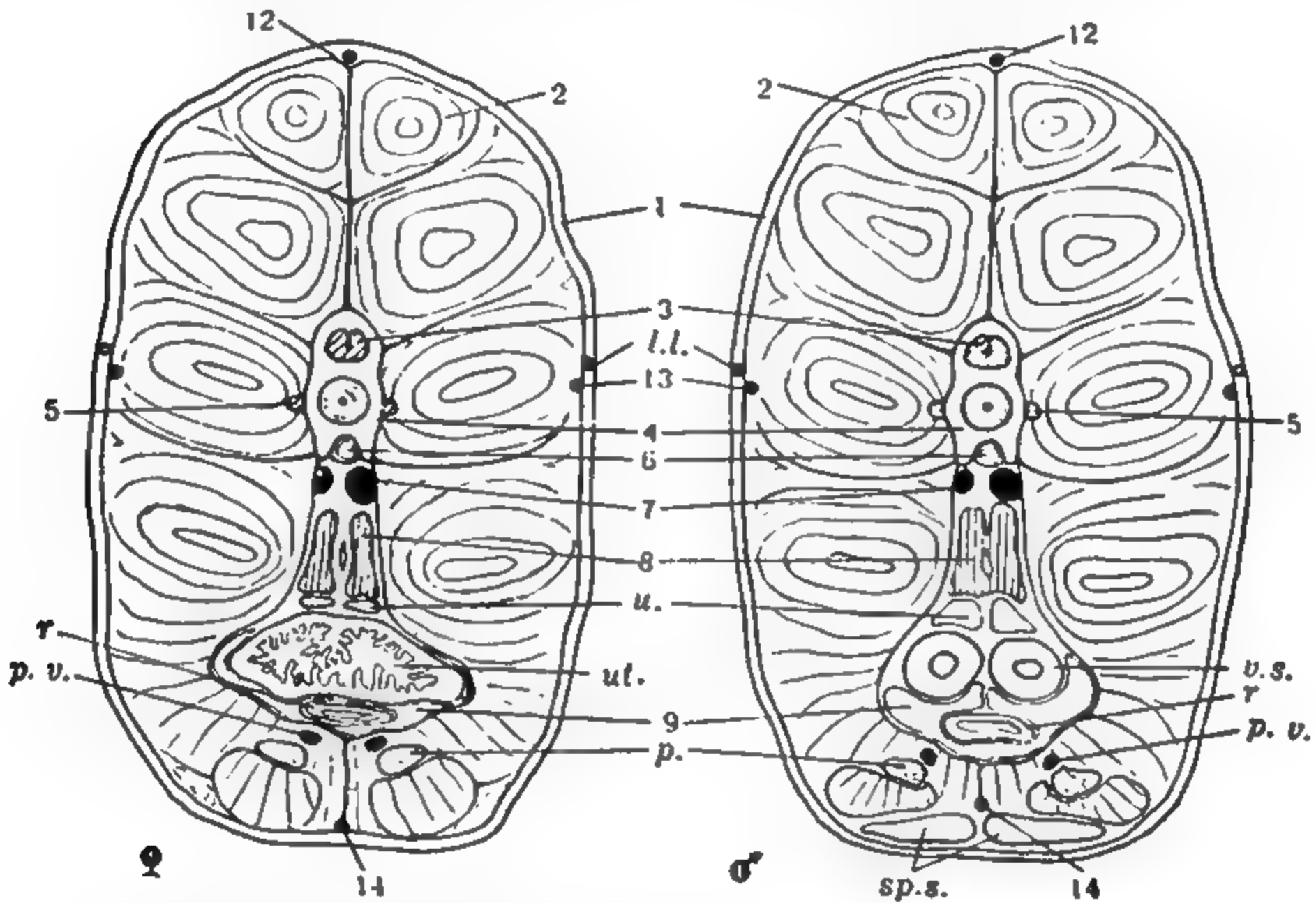
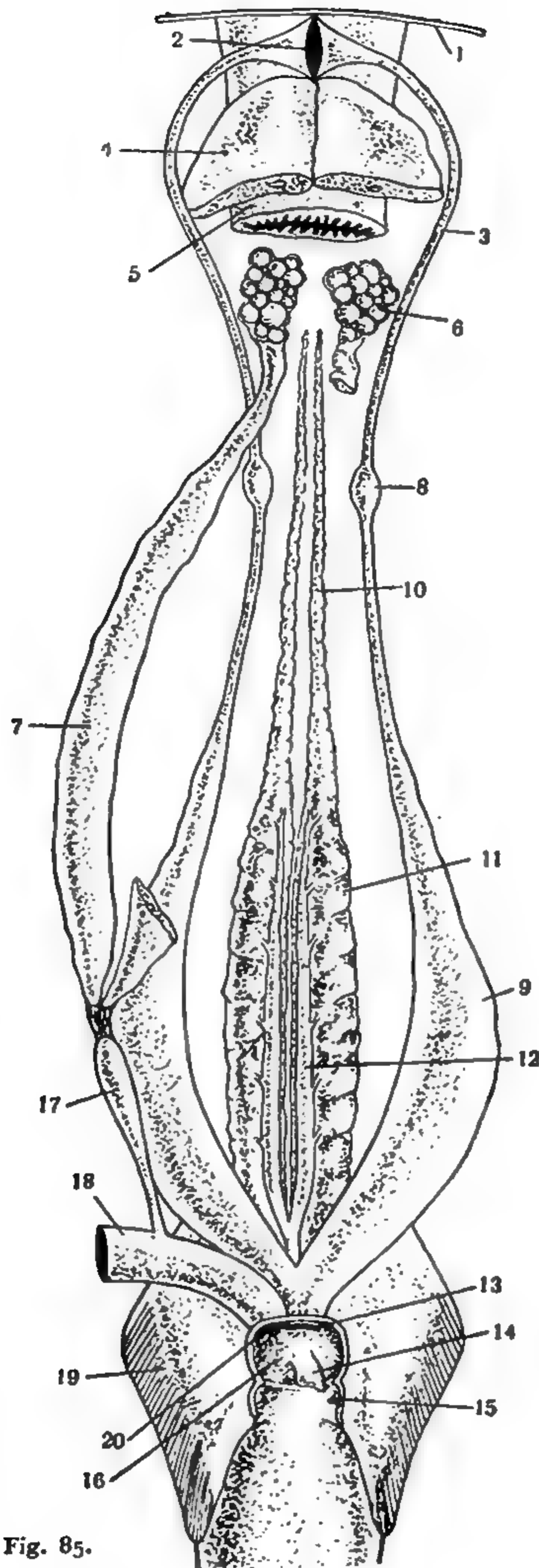


Fig. 84—Transverse sections of the body passing through the base of the pelvic fins of a male and a female shark. 1, integument; 2, myotomes; 3, spinal cord; 4, vertebra; 5, spinal nerve; 6, dorsal aorta; 7, posterior cardinal vein; 8, kidney; 9, coelom; 12, dorsal cutaneous vein; 13, lateral cutaneous vein; 14, ventral cutaneous vein; *l.l.*, lateral line canal; *p.*, cartilage of the pelvic fin; *p.v.*, iliac vein; *r.*, rectum; *sp.s.*, siphons; *u.*, ureter; *ut.*, two uteri fused together; *v.s.*, vesicula seminalis.

the ovaries are distinguished by the great size of the follicles enclosing mature ova. The *oviducts* or *Mullerian ducts* begin from the pericardio-peritoneal septum and extend through the entire length of the body-cavity, uniting behind to form the *vagina* which opens into the cloaca. Anteriorly the two ducts converge in the mid-dorsal line near the base of the liver and open into the coelom by a large median longitudinal slit, the *oviducal funnel*. The oviducts have no direct connection with the ovaries, so that mature ova are at first shed into the abdominal cavity, and later forced by the action



♀
Fem.

Fig. 85.

of the body-muscles into the oviducts through the single oviducal funnel. Just behind the funnel, the oviducts curve round towards the mid-dorsal line until they enlarge to form the small *shell-gland*, which is merely a dilated portion of each oviduct. Fertilization of mature eggs takes place in the section of the oviduct between the oviducal funnel and the shell-gland.

In oviparous forms like *Scyliorhinus* the shell-gland is of immense size, consisting of a dorsal and a ventral half, each of which is again divided into anterior and posterior areas, one portion secreting the albumen of the egg and the other the shell. But in *Scoliodon* the shell-gland is of little importance.

In *Scoliodon* and all other viviparous forms which give birth to living young, the posterior region of the oviduct dilates into a very wide chamber, the *uterus*, which serves as a place for the development of the young. During the breeding season the two uteri, occupying the greater part of the abdominal cavity, may contain many embryos, each of which may attain a total length of about 75 cm. before birth. The number of embryos seems to vary: in *Scoliodon palasorrah*, three embryos have been found in one uterus (fig. 87), but in *Scoliodon sorrakowah* as many as seven embryos have been seen in one uterus. The mucous lining of the uterus becomes divided into as many compartments as there are embryos within the uterus. Each of these compartments is filled with a fluid which completely surrounds the embryo and protects it. Posteriorly the two uteri unite to form a median chamber, the *vagina*, which opens into the cloaca by a large aperture. A fold of the mucous membrane of this region separates the vagina from the cloaca, and acts as a valve which closes the vagino-cloacal aperture during the development of the embryos within the uterus.

Fig. 85—The female urinogenital organs, 1, septum transversum or pericardio-peritoneal septum; 2, oviducal funnel; 3, oviduct; 4, liver; 5, oesophagus; 6, ovary; 7, epigonal organ; 8, shell-gland; 9, uterus; 10, anterior region of the kidney; 11, posterior region of the kidney (opisthonephros); 12, ureter; 13, opening of the uteri into the cloaca; 14, urinary papilla; 15, abdominal pore; 16, cloaca; 17, rectal (caecal) gland; 18, rectum; 19, pelvic fin; 20, opening of the rectum into the cloaca.

CHAPTER XII

THE DEVELOPMENT

In *Scoliodon*, as in other living Elasmobranchs, fertilization is internal. Agassiz (1871) discovered that during copulation one or both of the claspers of the male are inserted into the cloaca of the female and are fixed in position by the erection of the terminal pieces, while the spermatic fluid is forced through the grooves of the claspers into the oviducts through the vagina¹, fertilization taking place in the region of the oviducts in front of the shell-glands.

In the early stages of development each embryo is provided with a tubular *yolk-stalk* which is connected at one end with the gut of the embryo and at the other with a *yolk-sac* containing yolk for the nourishment of the young. In later stages when the yolk is more or less used up, the yolk-sac becomes greatly folded and embedded in the uterine wall, thus forming a *yolk-sac placenta*, through which the embryo obtains nourishment from the uterine tissues. With the formation of the placenta the tubular connection of the yolk-stalk with the gut becomes obliterated, but blood-vessels are developed in the yolk-stalk which thus becomes the *placental cord* attached to the embryo in the mid-ventral line at a point in level with the anterior edges of the pectoral fins. The other end of the cord ends in the folds of the yolk-sac placenta, which is usually attached close to the vaginal end of each uterus. The placental cord is twisted round each embryo; the head of the embryo points forward while the tail is bent on itself (fig. 87). Each embryo has its own placental cord and placenta. A dissection of the placental cord reveals an artery which can be traced to the dorsal aorta of the embryo, and a vein which opens into its hepatic portal vein; at the other end, these blood-vessels end in those of the placenta which is now highly vascular. From the placental cord grow out numerous delicate tubular processes, the *appendiculæ* which were first described and named by Alcock². Each appendiculum consists of several layers of epithelial cells surrounding a central core of loose connective tissue.

¹ Bolau, H.—"Paarung und Fortpflanzung der *Scyllium*-arten," *Zeit. wiss. Zool.*, Bd. 35, 1881.

² Alcock, A.—"Some Observations on the Gestation of some Sharks and Rays," *Journal of the Asiatic Society of Bengal*, LXIX (ii), 1890.

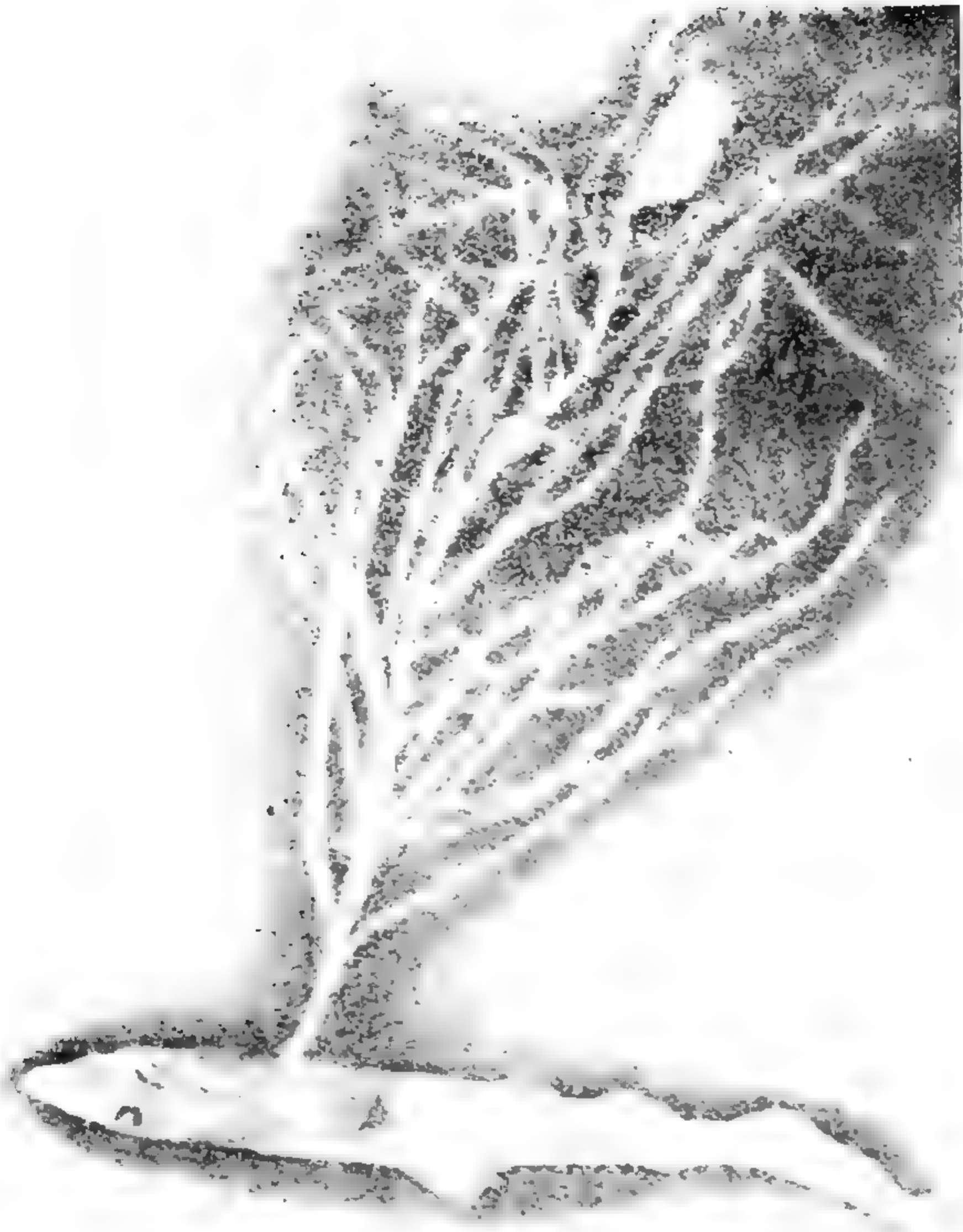


Fig. 86—An embryo of *Scoliodon sorrakowah* taken out of the uterus showing the place of attachment of the placental cord, long filiform appendicula and the yolk-sac placenta.

Southwell and Baini Prashad¹ describe four types of appendicula amongst the sharks of the Indian Seas:

(i) In a species of *Scoliodon* from Ceylon, the placenta is of the usual arborescent type and the placental cord is very long (19 c.m.) and fairly thick (5mm. in diam.). The wall of the placental cord is thrown into folds which are quite separate at places to form small flat processes. These processes seem to be the starting point for the formation of the more highly evolved types of appendicula.

(ii) In *Scoliodon walbeehmi*, the whole surface of the cord is covered with appendicula which are small and flattened tubular processes, broad at their distal but narrow at their proximal ends.

(iii) In *Scoliodon palasorrah*, the placental cord is over 70 m.m. in length and is thickly covered with appendicula which are much branched. The primary branches arise from a main axis, but the secondary branches are more or less dichotomous. Each branch is swollen at its extremity (fig. 87).

(iv) In *Scoliodon sorrakowah* (fig. 86) the appendicula are elongated threads which are either simple or are forked at a distance from their point of origin. Each of these appendicula has a blood-vessel in it.

They also record three types of placenta:

(i) In *S. palasorrah* and *S. sorrakowah* the placenta is least modified; it is the original yolk-sac of the typical ovoid form. At its lower extremity it has a number of small protuberances which are imbedded in the maternal uterine tissues and form a very simple type of yolk-sac placenta.

(ii) Muller describes a more advanced type in *Mustelus laevis* and in a species of *Carcharias*, in which there is a distinct placenta-like interdigitation of the folds of the yolk-sac and corresponding depressions in the uterine mucous membrane of the mother, like the cotyledons of the placenta of Ruminants.

(iii) In *Scoliodon walbeehmi* the yolk-sac practically disappears but the distal end of the placental cord broadens out to form a flattened structure showing traces of division and transformation into an arborescent mass.

It is significant that in species with the best developed appendicula, the placenta is vestigial, which seems to show that in these forms the appendicula probably aid in the absorption of nutritive material secreted by the uterine wall of the mother, since it cannot be done efficiently by the vestigial placenta.

HISTORY OF OUR KNOWLEDGE OF SELACHIAN DEVELOPMENT

It is an interesting fact that even Aristotle² (384 B. C.—322 B.C.) knew that although fishes as a whole were oviparous, there were some Selachians that were viviparous. He says, "Some animals are viviparous, such as man, the horse, the seal and all other animals that are hair-coated; and, of marine animals, the cetaceans as the dolphin, and the so-called *Selachia*³"

¹ Southwell and Baini Prashad—Notes from the Bengal Fisheries Laboratory, No. 6, Embryological and Developmental studies of Indian Fishes, Records of the Indian Museum, vol. XVI, 1919.

² This account of the history of the discovery of Selachian development is taken from Charles Singer's "Studies in the History and Method of Science," vol. II, Oxford, 1921.

³ *Historia Animalium*, 5; 489b 35.

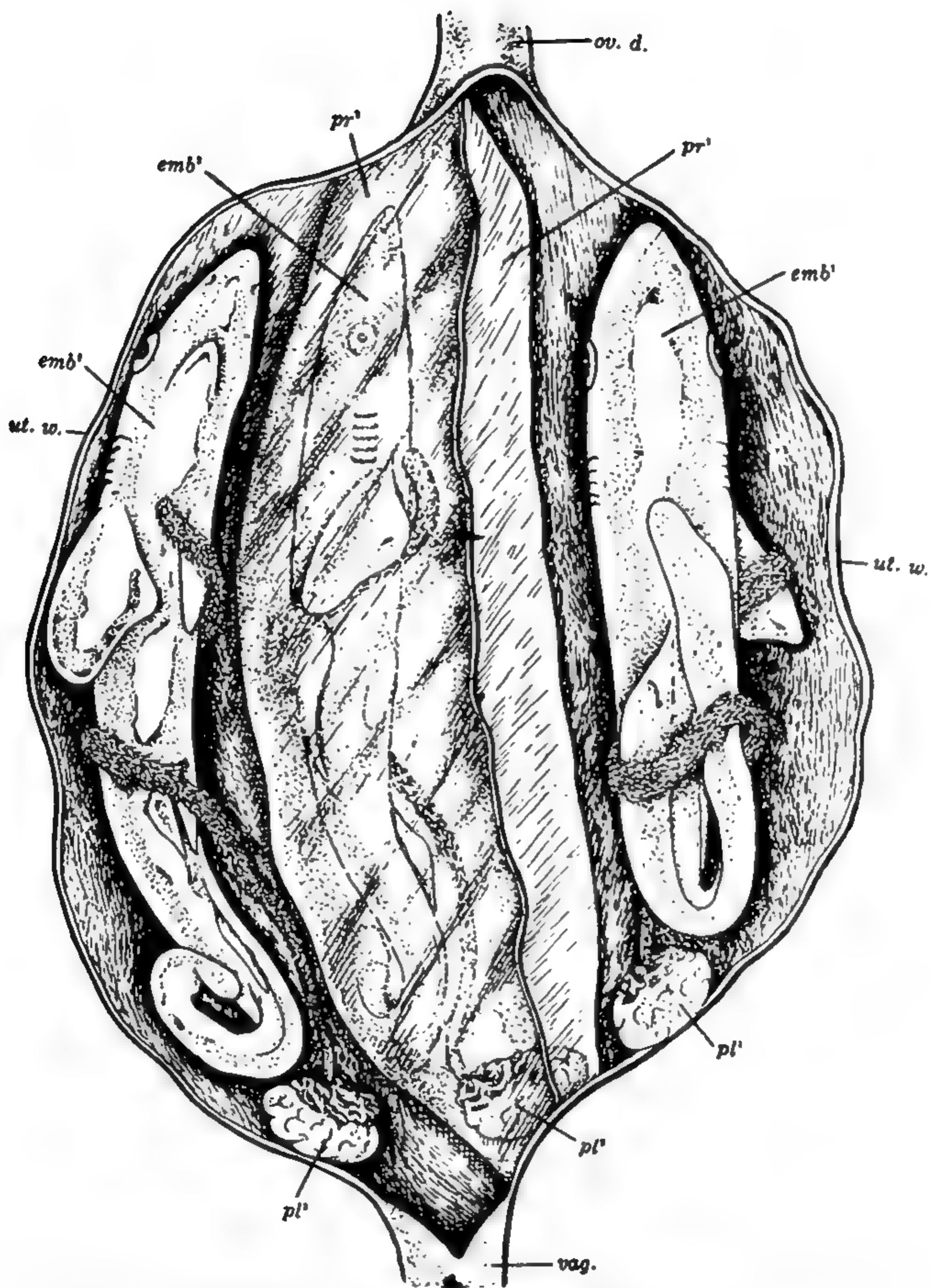


Fig. 87—The right uterus of *Scoliodon palasorrah*, cut open to show the embryos within, *emb¹*, male embryo; *emb²* and *emb³*, two female embryos; *ov. d.*, anterior end of oviduct; *pl¹*, *pl²*, *pl³*, yolk sac placentae attached to the wall of the uterus and to their placental cords; *pr¹*, *pr²*, intra-uterine partitions between embryos; *ut. w.*, uterine wall; *vag.*, vaginal end of uterus.

In the sixteenth century Pierre Belon (1553) and Guillaume Rondelet (1554) were the first to recognise the placental attachment of the Selachian foetus to the uterus of the mother. Belon's work was copied by Aldrovando in a work published in 1613, which came into the hands of Stensen, who definitely determined the relationship of the Selachian embryo to the maternal uterus in 1625. Stensen's observations were long disregarded but in 1828 Cuvier in his work on fishes briefly remarked that in *Carcharias* the yolk-sac is attached to the uterus as firmly as a placenta. It is strange that neither Stensen nor Cuvier referred to Aristotle on this subject, so that the importance of this ancient discovery was unappreciated by the world, until Johannes Muller in 1839 showed that *Carcharias* and *Mustelus* exhibited a peculiar placental development. At the same time he demonstrated the fact that within the genus *Mustelus*, one species, *i.e.*, *M. Laevis* has the foetus firmly united to the uterus by means of a placenta, while in another species, *i.e.*, *M. vulgaris*, the yolk-sac is quite free and unattached. Later observers have shown that embryos of many of these are nourished from other sources when the yolk is consumed. The nutritive material in some cases is secreted by the uterine wall and taken directly into the mouth of the embryo, or through the gill-slits, or is absorbed by the blood-vessels of the yolk-sac. In some forms the walls of the uterus develop secreting villi which pass through the spiracles of the embryo, while in others, as in *Scoliodon*, a placenta is actually developed, and the process of absorption is aided by appendicula which occur on the placental cord throughout its length.

It is further interesting to note that Aristotle even attempted to give an explanation of the viviparous condition in Selachians. "Birds and scaly Reptiles," he says, "because of their heat produce a perfect egg, but because of their dryness, it is *only* an egg; the cartilaginous fishes have less heat than these but more moisture, so that they are intermediate, for they are both oviparous and viviparous within themselves, the former because they are cold, the latter because of their moisture; for moisture is vivifying, whereas dryness is furthest removed from what has life. Since they have neither feathers nor scales such as either reptiles or other fishes have, all of which are signs rather of a dry and earthy nature, the egg they produce is soft; for the earthy matter does not come to the surface in their eggs any more than in themselves. That is why they lay eggs in themselves, for if the egg were laid externally it would be destroyed, having no protection."

"Aristotle's explanation may seem meaningless to modern ears just as many of our modern theories may seem absurd to future generations. Such explanations, however, are worth recording not only as a stage in the historical development of biological theory but also as illustrating the fact that while the function of science is the description of nature, its motive is almost always the explanation. It is usually the descriptive and not the explanatory element that bears the test of time.

CHAPTER XIII

ANCESTRY, BIONOMICS, DISTRIBUTION AND RELATIONSHIPS

It is generally believed that life began in the sea, and since the protochordates and the lower living vertebrates are mainly inhabitants of the sea, it was assumed for a long time that fishes were descended from marine ancestors. But recent analysis of the habitats of early fossil fishes by Romer and Grove¹ has led to the conclusion that the vertebrates were originally a freshwater group. The earliest vertebrates, *i.e.* the Ostracoderms (Agnatha) were entirely inhabitants of fresh waters in Ordovician times and remained so to the end of their history in the Devonian, although there was some tendency towards a marine life in the Heterostraci. The Aphethoidea (Placodermi) were likewise of freshwater origin, but while the Antiarchi remained in freshwater, the Arthrodira in the lower Devonian migrated almost entirely into the sea. The oldest shark-like fishes, the Acanthodians, originated in freshwaters of the Upper Silurian and remained there to the end of their history in the Lower Permian, but the other groups of Placoderm sharks began to migrate to the sea about the beginning of the Devonian. The origin of the Chondrichthyes is still obscure. Romer¹ thinks that these marine sharks are descended from freshwater Acanthodians, while Moy-Thomas² thinks that they may be 'paedomorphic' descendants of one of the Placoderm families which have retained their larval cartilage. Similarly, the higher (bony) fishes originated in freshwaters in which their evolutionary centre remained throughout the Devonian period. The palaeontological evidence, therefore, is indisputably in favour of the freshwater origin of fishes. Further, the active swimming habit which characterizes the early vertebrates suggests that their home lay in fresh waters where mobility was necessary to counteract the downward sweep of stream currents.

The freshwater origin of fishes has been independently confirmed by a study of the physiology of their excretion by Homer

¹ Romer, A.S. and Grove, B.H.—Environment of the early vertebrates, *American Midland Naturalist*. vol. 16, No. 6, 1935.

² Moy-Thomas, J.A.—*Palaeozoic Fishes*, London, 1939.

Smith¹. Freshwater animals are osmotically independent, *i.e.* they are liable to maintain a constant internal salinity higher than that of freshwater; they have semi-permeable membranes through which water is continually passing into the animal, but the danger of water-logging is avoided by excreting the incoming water as fast as it enters, in the form of a copious but very dilute urine through the excretory organs, *e.g.* nephridia or kidneys. In vertebrates the presence of a water-excreting device in the form of a "glomerulus" in the kidney is evidence of their freshwater ancestry². The glomerulus has persisted in the elasmobranch kidneys, although these fishes have now migrated into the sea. In this denser medium, loss of water from the body has been prevented by the retention of urea (2 per cent or more) in the blood (physiological uraemia), which raises the osmotic pressure to a level slightly higher than that of sea water. This water is freely excreted in their hypotonic urine. Some of the elasmobranchs³, *e.g.* *Pristis*, *Dasyatis* and *Potamotrygon* have gone back to freshwater but they have carried with them a legacy from their past marine life in the form of uraemia, although the urea content is now reduced to 0.6 per cent (pages 68-69).

As a group sharks are distinguished by their muscular strength, the activity of their movements and the acuteness of their sight and smell.

The natural home of the sharks of the present day are the seas and estuaries of the tropical regions where they are most numerous, but they are not of uncommon occurrence in the temperate and even arctic regions, *e.g.* various species of the tiger-shark *Galeocerdo* have a wide distribution in the arctic, temperate and tropical seas. Not many years ago the Timor Sea in the north of Australia had the reputation of being the area most infested with sharks in the vast Indian Ocean, but the Australian government launched a campaign to clear the long dreaded Timor Sea of sharks, in order to make the air route from England to Australia as safe as possible. Some sharks, like the zebra shark *Stegostoma*, are littoral in habit and keep close to the coasts and harbours, but most of them love the open sea and roam over great expanses. A few, like the goblin-shark *Scapanorhynchus* (*Mitsukurina*), are found in the deep seas where no light enters;

¹ Smith, Homer W.—Lectures on the kidney, University of Kansas, Lawrence, Kansas, 1943.

² Marshall, E.K. & Smith, Homer W.—The glomerular development of the vertebrate kidney in relation to habitat. *Biological Bulletin*, vol. 59, 1930.

³ Homer Smith has recorded *twenty* genera with *fifty-three* species as freshwater elasmobranchs. (Smith, Homer W.—The retention and physiological role of urea in Elasmobranchii, *Biological Reviews*, 1936).

some ascended large rivers and seem to be perfectly at home in fresh water, e.g. the Ganges shark *Carcharhinus gangeticus* which is one of the most ferocious of Indian sharks and has a wide distribution from the seas of India to Japan, ascends large rivers, like the Ganges and the Tigris, even above tidal influence; in the Hooghly at Calcutta it is a great menace to bathers, while in the inland lakes of Fiji it is entirely an inhabitant of fresh-water; the Zambesi shark *Carcharinus zambesensis* has been captured about 120 miles above the mouth of the river; while *Carcharinus nicaraguensis* of Lake Nicaragua and its outlet Rio San Juan in Central America is confined entirely to fresh water.

The commonest species of sharks found along the coasts of India belong to the genera *Scoliodon* and *Carcharinus* and are very destructive to herrings and other edible fish. It has been observed that one of the remarkable results which followed the construction of the Suez Canal was the introduction into the Mediterranean Sea of sharks which were formerly almost unknown there.

The size which the sharks attain is very varied: some of them, like *Scoliodon sorrakowah*, are only about two feet long, while some of the giant sharks of the present day attain great lengths, e.g. the great white shark or man-eater *Carcharodon* grows to a length of 40 ft. or more, while the whale shark *Rhineodon* is known to exceed 50 ft. in length.

All sharks are carnivorous but their food varies from small pelagic organisms to fishes, marine mammals and even human beings. The basking shark *Cetorhinus* and the whale shark *Rhineodon*¹ have small teeth and feed on small pelagic crustaceans, larval fishes etc.; the nurse shark *Ginglymostoma* and the hound shark *Mustelus* have small pointed or flattened teeth adapted for grinding and crushing shell-fish, crustaceans and small fishes; while the tiger-shark *Galeocerdo* has large sickle-shaped teeth and preys upon porpoises, dolphins, sea-birds, turtles, crabs, squids, shell-fish, sharks and other fishes of all kinds. Jordan has described a man-eater (*Carcharodon*) with a good sized sea-lion in its stomach, while the stomach of another specimen of this shark contained a tin-can, a number of mutton bones, the hind-quarters of a pig, the head and fore-quarters of a bull-dog and a quantity of horse-flesh. The Ganges shark *Carcharinus gangeticus* is specially fond of living human flesh; not infrequently does it seize

¹ Gudger, E. W.—The feeding organs of the whale shark *Rhineodon typus*. *Journal of Morphology*, vol. 68, 1941.

the arm or leg of an incautious bather, although generally it feeds upon corpses and is a scavenger.

In sharks the sexes are separate and fertilization is internal, the ova being fertilized within the oviduct. The Greenland shark *Somniosus* lays small eggs quite unprotected by a horny envelope; *Scyliorhinus* and *Cestracion* are also *oviparous*, but their eggs are encased in a horny case before being deposited in the sea; while *Scoliodon*, *Carcharinus*, *Carcharodon Rhineodon* and *Galeorhinus (Mustelus)* are *viviparous*, the development of the egg taking place within the oviduct, and the young being finally born alive in an advanced condition. In a great many viviparous forms there is a placenta-like connection between the growing embryo and the oviduct of the mother, serving to aid in the nutrition and respiration of the embryo. In the nurse shark *Ginglymostoma* there is an intermediate condition between the simple oviparous and the highly specialized viviparous condition: when the eggs after fertilization reach the shell-glands, they are enveloped in brownish-black horny cases; the eggs in these egg-cases travel behind into the "uterus" of the female and there undergo development within their respective shells; the fully formed young hatch out by breaking the shell while still within the uterus and thence emerge into the sea through the cloaca: such a condition is described as *ovo-viviparous*.

Although sharks and skates are not considered as palatable as some other fishes, they find a fair market among people who cannot afford to pay the high price demanded for other edible fishes, like the pomfret (*Stromateus*) and the Bombay Duck (*Harpodon*). Along the sea-coasts of Southern India and Ceylon, the poorer classes eat sharks and rays, while in Bombay they are salted and sold to the African sailors. Unfortunately there is a prejudice against sharks based on the old mistaken belief that all sharks are man-eaters. As a matter of fact, if some of the sharks and skates are properly prepared, they compare in edibility very favourably with the more popular fishes.

Shark fin-soup is greatly relished by the Chinese and Filipinos. Several tons of dried fins are exported every year from the large sea-ports of India to China. In preparing the fins for use, the Chinese soak them in warm water until the flesh softens and the cartilaginous rays can be separated out; these rays keep indefinitely when dried and are sold in retail stores. They are sliced up and boiled with chicken, beef or mutton in the preparation of soup¹.

¹ Walford, Lionel A.—The Sharks and Rays of California. Fish Bulletin, No. 45, California State Fisheries Laboratory, 1931.

"With the bony dermal denticles *in situ*, the crude skins of sharks and dogfishes are used by carpenters and cabinet makers for smoothing and polishing, as well as by metal workers; suitably prepared and dried skins provide the *shagreen* used for covering car-cases, jewel boxes, sword scabbards and for ornamental work of all kinds. After being specially tanned and having had the dermal denticles removed, the skins of most sharks and rays provide strong and highly durable leather, and with the increasing demand for this commodity in recent years the shark leather industry is fast becoming a satisfactory commercial proposition¹ "

The livers of many sharks and rays yield large quantities of oil, which is used for the curing of leather, for making tarpaulins and other oil cloths, for manufacturing low grade soaps, for tempering steel and for mixing with vegetable oils for paints. In Greenland, shark oil is used for illuminating purposes. In Europe, parts of Asia and sometimes in the United States, shark liver oil is sold as a substitute for the cod liver oil.

Sharks mixed with fish offal of canneries are manufactured into a fertilizer, while crushed and ground bones make a special kind of manure.

In most places sharks are captured by baits attached to rough hooks and fixed to a chain, but along the east coast of India Reduce nets of strong twine, a quarter of a mile or more in length, are used. The nets are sunk in a depth of 80 to 150 ft. out in the open sea.

The Elasmobranchs form an ancient group of fishes which constituted a very important section of the fauna of the Palaeozoic epoch, the modern elasmobranchs being the survivors of this Palaeozoic race. The earliest remains of these fishes appear in the form of dermal denticles and teeth, called *ichthyodorulites*, as far back as the Upper Silurian rocks. The origin of the Selachians is obscure but recent researches of Stensio and Kiaer have revealed a group of armoured jawless vertebrates (*Heterostraci—Agnatha*) which may be ancestral to the Elasmobranchs. Probably the most primitive elasmobranch ancestor known is the small marine *Macropetalichthys* (Lower Devonian) which was an armoured shark retaining a dorsal shield composed of several bony plates, but with an endoskeleton distinctly on the elasmobranch plan; there are no unpaired fins, but the paired fins are large and have complete endoskeletal supports. An allied form, *Cratoselache*, occurs as late as the Carboniferous.

¹ Norman, J. R.—A History of Fishes, 1931 P. 401.

Occurring about the same period as these Stegoselachians are the *Rhenandina*, of which *Gemundina* is an example. This form shows a reduction of the exoskeletal armour but the endoskeleton is plainly on the elasmobranch plan. The first true elasmobranchs (*Pleuropterygii*), in which the external armour is reduced to a covering of dermal denticles and dorsal fin-spines, have been found earliest in the Upper Devonian of Ohio; the best known example is *Cladoselache* (fig. 1), a shark with an unconstricted notochord and paired fins with unsegmented parallel radials, but differing from modern sharks in the absence of claspers. Its broad-based pointed fins and strongly heterocercal tail suggest that it was a powerful swimming shark. It became extinct at the close of the Devonian period.

Of the sub-class *Ichthyotomi* the best known genus is *Pleuracanthus* (fig. 4) which flourished for a short time but whose well-preserved skeletons have been found in the Carboniferous and Permian rocks of Europe, Australia and North America. The paired fins had a segmented axis with radials arranged on either side, the notochord was unsegmented and the tail was diphyccercal. This shark had claspers and a long median spine projecting from the back of the head. It was a feeble swimmer and probably lived at the bottom of the sea.

The *Bradyodonti* are a group apart which probably lead to the modern chimaeras. Their broad-based teeth were crowded together to form flat pavements for effectively crushing molluscan shells.

CHAPTER XIV

DIRECTIONS FOR PRATCTICAL WORK

Sharks that are sent out from the Ennur Fisheries Station and other supply stations to the different universities in India are preserved in formalin. Only the universities on the sea-coast like those of Madras, Bombay, Andhra, Trivandrum and Colombo are able to get fresh sharks for dissection. As a complete dissection of all the systems takes several days, sharks should be kept in 6 to 7% formalin for use day after day and washed in water immediately before dissection.

Besides making a careful dissection, a series of hand-cut transverse sections through different regions of the body should be carefully examined and sketched. These sections are very instructive and give a very good idea of the relations of the different parts of the body.

1. *External characters.* Before attempting the dissection the student should carefully examine the external characters, such as the general shape of the body, the position and number of fins, the location of the receptor organs, and other features shown in fig. 43, P. 15.

2. *Placoid scales.* In order to make a preparation of the scales, a small piece of skin should be placed in 40% solution of caustic potash for a few minutes. It may be gently heated over a gas flame, if necessary, in order to isolate the scales. The test-tube containing the scales should not be shaken, or else the scales will get broken. The scales should then be washed in water and mounted in glycerine, or passed through strong alcohol, dried and mounted in balsam (fig. 45, P. 19).

3. *Teeth.* The succession of teeth and their relation to the placoid scales can best be studied by examining a transverse section through one of the jaws under a dissecting microscope (fig. 57, P. 43). Some of the teeth should then be detached from the jaws, cleaned, and mounted on a slide and examined under the low power of microscope (fig. 43B, P. 15).

4. *Muscles.* If a part of the skin from the side of the body is removed, the zig-zag arrangement of the body-muscles is revealed (fig. 43, P. 15), while transverse sections of the trunk and tail show

the concentric arrangement of the muscle-lamellae (fig. 60, P. 48). A small piece of muscle should be teased out in water, stained with methyl green and examined under the microscope.

5. *Preparation of the skeleton.* The skeleton is best prepared from a full-sized shark which has not been hardened in formalin. For this purpose, fresh specimens packed in saw-dust should be ordered. As the skeleton is cartilaginous, it is easily damaged and should, therefore, be cleaned with care. After the skin and muscles have been removed, the specimen should be dipped in hot water to loosen the connective tissue that binds the parts together. The skull and visceral skeleton require a great deal of care, as many delicate cartilages are likely to be broken if handled roughly. The student should have figs. 47, 48, 49 and 50 before him when these parts are being prepared. The vertebral column is best studied by making transverse and vertical longitudinal sections (fig. 46, page 21), but the median fins should be separated and their attachments to the vertebral column noted before the sections are taken (fig. 52, page 33). In cleaning the paired fins, care should be taken to note the relation of the pectoral girdle to the heart, and that of the pelvic fin of a male to its clasper and siphon-tube (fig. 53, P. 34; fig. 54, P. 35). All the parts of the skeleton thus prepared should be kept in weak formalin, since the cartilage dries up easily on exposure to air.

6. *Dissection of the abdominal viscera.* The fish should be pinned down to the dissecting board with the ventral side uppermost; this is done by passing strong nails obliquely through the pectoral and caudal fins. The abdominal cavity is opened by a median ventral incision, extending from the anterior border of the pelvic to the posterior border of the pectoral girdle. Transverse cuts along the line of the pectoral and pelvic girdles completely expose the internal viscera. After the flaps have been pinned down to the dissecting board, the student should locate the position and relations of the various organs by following the description in the text (fig. 58 P. 45). In order to get a full view of the cloaca, the pelvic girdle should be cut and the opening partially stretched out to display the apertures. When all the structures of the abdominal cavity have been identified, the alimentary canal should be separated from the mesentery and opened out by a longitudinal slit along its whole length, its contents should be washed thoroughly in water, and the folds of the mucous membrane of the various regions of the canal observed (fig. 59, P. 47). A transverse section of the intestine shows the turns of the scroll-valve. The *bile duct* should be traced from the liver through the mesentery to the intestine, and its opening observed

by injecting the duct with carmine (fig. 59, P. 47). The *pancreatic duct* can be traced in a similar manner from the pancreas to the intestine.

Microscopic sections through the stomach, intestine, liver, pancreas, spleen and other organs should be examined under the microscope.

7. *Gills.* A mid-ventral incision of the floor of the buccal cavity and pharynx will expose the pharyngeal openings into the gill-pouches, while a section through a holobranch examined under a dissecting microscope will show the relations of the different parts and the blood-vessels of the gills, specially if the blood-vessels are injected with carmine before the section is taken (fig. 62, P. 53). The position of the gill-less spiracular pit in front of the functional gill-pouches should also be noted.

8. *Heart.* The chambers of the heart should be dissected to compare the thickness of their walls, specially the thick and spongy texture of the ventricular wall with the thin walls of the sinus venosus, and to make out the semi-lunar valves and accessory valves in the conus arteriosus (fig. 63).

9. *Injection and dissection of the blood-vessels.* The dissection of the blood-vessels is greatly facilitated by injecting the vessels of a fresh shark with a coloured fluid. Fine plaster of Paris, coloured with vermilion or carmine, is an excellent injecting material. "French blue" mixed with glycerine, starch, and methylated spirits in definite proportions forms an injection-fluid¹, that will keep for an indefinite period in a tightly closed bottle. The vessels injected should be tightly ligatured at their cut ends, and the specimen preserved in methylated spirits for a few hours, and finally transferred to a weak solution of formalin. This will harden the tissues and the injection fluid will set in the vessels and bring out their outline and course of distribution clearly.

A satisfactory injection of the arteries of the branchial region and the head can be made by cutting the dorsal aorta immediately behind the epibranchial arteries and injecting forward by inserting the nozzle of the syringe into the cut end of the aorta which should be tightly ligatured after injection; the blood-vessels of the gut can be injected easily through the coeliaco-mesenteric artery, and the

¹ 4 gms. of "French blue" ground with 4 c.c. of glycerine and an equal quantity of methylated spirits should be mixed with 50 gms. of starch in 50 c.c. of water and 25 c.c. of methylated spirits.

arteries of the posterior region can be similarly injected through the dorsal aorta backwards (figs. 64 and 65).

The veins enlarge into irregular sinuses and are rather difficult to inject. The veins of the kidneys can be injected through the caudal vein, while the lateral vein can be injected by opening one of these veins in the abdominal cavity, and directing the syringe towards the heart; the inferior jugular sinus can be injected either from the ventral ends of the hyoidean sinus or from the Cuvierian sinus by pushing the syringe beyond the valve; the anterior cardinal sinus and the other veins of the head can be injected in the same way. To ascertain the precise position of the chief vessels in relation to the parts surrounding them, and to determine the correct position of the cutaneous vessels, transverse sections through the various regions of the body are very instructive; these should be made from specimens that have been previously injected and hardened (figs. 67 and 68).

10. *The receptor organs.* The receptor organs and the nervous system can be dissected on the same specimen, but the receptor organs should be dissected first in the following order:

(i) *Pit-Organs.* The pit organs are groups of small openings on the dorsal surface of the head behind the eyes; these can be seen by means of a hand-lens (fig. 81).

(ii) *Ampullae of Lorenzini.* The pores of the ampullae are visible in groups on the dorsal and ventral surfaces of the head (fig. 81); on slightly pressing the skin of these organs, a mucous substance exudes from them. If the skin of the head is carefully removed and examined under a binocular microscope through transmitted light, these pores are clearly seen. In order to make out the structure of the ampullae and their nerves, a bunch of ampullae should be removed, teased out on a slide in dilute glycerine and examined under the microscope (fig. 82).

(iii) *The lateral line and cephalic canals.* The cephalic canals are closely connected with the ampullae and can be dissected out on the head by scraping off the outermost layer of the integument. This dissection is not easy and the beginner may find it difficult at first, but if the dissection is made carefully, all the connections of the canals can be traced (figs. 74, 79 and 80). The lateral line canals lie on either side of the body but are more deep-seated and are easily exposed without injury by a careful removal of the skin from the body-wall.

(iv) The *olfactory organs and the nasal flaps* (figs. 75 and 76), (v) the *eye and the eye-muscles* (fig. 77), and (vi) the *membranous labyrinth* (fig. 78) should then be dissected out on one side.

11. *The brain and the peripheral nervous system.* In order to dissect out the nervous system, the cartilage of the cranial roof should be partly removed and the entire specimen immersed in formalin or methylated spirits for a few days. This hardens the tissues and facilitates the dissection. When the specimen is removed from the hardening fluid, it should be thoroughly washed in water, but should be kept moist with a sponge throughout the dissection in order to prevent drying of the tissues. Enough of the cranial roof should be removed in order to expose the brain, after which the cranial nerves and their branches can be traced from their origin to their destination (figs. 73 and 74). When the nerves have been traced, the brain should be removed from the cranial cavity, and if necessary, it may be hardened further in chrom-acetic solution. Sections of the brain, horizontal and vertical, should be made and compared with the diagrams in the text (figs. 69-72).

12. *The urinogenital organs.*

The *male urinogenital organs* (fig. 83). In a full grown specimen, the *testes* lying immediately beneath the liver can be easily distinguished. A piece of a testis teased out on a slide in salt solution and examined under the high power of the microscope will show the mature spermatozoa. The *vas deferens* and its relation to the kidney can be observed by dissecting out the tough fibrous peritoneum lining the roof of the coelom close to the vertebral column. The small tubules that pass from the testes to the kidneys (the *vasa efferentia*) can be seen with a hand-lens. Posteriorly, each *vas deferens* widens out into the *vesicula seminalis* which is easily dissected with the naked eye. The relation of the sperm-sacs to the urinogenital sinus as well as that of the siphon-tubes to the clasper-grooves should be noted.

The *kidneys* should be traced back to the posterior end and the relation of the ureters noted. A transverse section of the kidney examined under the microscope reveals the glomeruli and the kidney-tubules. The *urinogenital sinus* should be cut open, and the openings of the seminal vesicles and the ureters observed by injection or by passing a seeker through their openings.

The *female urinogenital organs* (fig. 85). The *ovaries* are minute in an immature specimen, but in the adult they are large and are easily

seen lying immediately beneath the base of the liver. Sections of the ovary under the microscope show the ova in various stages of development. The *oviducts* and their different regions should be traced out, and the position of the median oviducal funnel noted. The *kidneys* and the *ureters* can be dissected by removing the peritoneum as in the male. The difference in the extent of the kidneys in the two sexes should be noted. The *urinary sinus* should be opened and the openings of the ureters distinguished by injection or by passing a seeker through the sinus.

13. *Dissection of the intra-uterine embryos* (figs. 86 and 87). Gravid females should be obtained when possible and the uterus opened to see the relation of the developing embryos to the uterine wall, noting the embryonic structures, such as the *yolk-sac placenta*, the *placental cord*, and the *appendicula* with their special peculiarities in the different species of *Scoliodon*. Portions of the appendicula should be examined under the microscope.

CHAPTER XV

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